Morphology and molecular phylogeny of the cave dwelling subgenus Illyrionethes Verhoeff, 1927 (Isopoda, Trichoniscidae) in the Dinaric karst

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MORPHOLOGY AND MOLECULAR PHYLOGENY OF THE CAVE DWELLING SUBGENUS *ILLYRIONETHES* VERHOEFF, 1927 (ISOPODA, TRICHONISCIDAE) IN THE DINARIC KARST

DOCTORAL DISSERTATION

Supervisors:
dr. sc. Sanja Gottstein, dr. sc. Stefano Taiti

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Jana Bedek

MORFOLOGIJA I MOLEKULARNA FILOGENIJA TROGLOBIONTSKOG PODRODA *ILLYRIONETHES* VERHOEFF, 1927 (ISOPODA, TRICHONISCIDAE) U DINARSKOM KRŠU

DOKTORSKI RAD

Mentori:
dr. sc. Sanja Gottstein, dr. sc. Stefano Taiti

Zagreb, 2019

This doctoral dissertation was carried out as a part of the postgraduate programme at the University of Zagreb, Faculty of Science, Department of Biology, Division of Zoology, under the supervision of prof. Sanja Gottstein from the University of Zagreb, Faculty of Science, Department of Biology, Division of Zoology, and dr. sc. Stefano Taiti from the Istituto di Ricerca sugli Ecosistemi Terrestri, CNR, Florence, Italy. The majority of fieldwork was performed in the frame of the different projects carried out by the Croatian Biospeleological Society. The molecular part of the research and part of the taxonomic analysis were carried out at the Istituto per lo Studio degli Ecosistemi, CNR, Sesto Florentino – Italy, while the majority of taxonomic analysis was carried out at the Croatian Biospeleological Society, Zagreb – Croatia.

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Dr. sc. Sanja Gottstein

EDUCATION

2003 Ph.D. in Natural Sciences – Biology-Ecology, University of Zagreb (Croatia), Faculty of Science
1998 M.Sc. in Biological Sciences – Ecology, University of Zagreb (Croatia), Faculty of Science
1994 Diploma in Biology, University of Zagreb (Croatia), Faculty of Science

EMPLOYMENT

1995 – 1997 expert associate, University of Zagreb, Faculty of Science
1997 – 2007 Research and Teaching Assistant, University of Zagreb, Faculty of Science
2007 – 2012 Assistant Professor, University of Zagreb, Faculty of Science
2012 – on-going Associate Professor, University of Zagreb, Faculty of Science
2019 – on-going Full Professor, University of Zagreb, Faculty of Science

SUPERVISION OF DOCTORAL STUDENTS AND POSTDOCTORAL RESEARCHERS

From 2007 to 2019 under her supervising three postgraduate students were defended MSc work, and three PhD students were defended doctoral thesis.

TEACHING ACTIVITIES

Experience in high education dealing with biospeleology, groundwater ecology, distributional ecology, biogeography, taxonomy, phylogeny and biodiversity of epigean and subterranean crustaceans, environmental impact studies in freshwater ecology, habitat mapping and freshwater invertebrate inventory.
2016 – teaching activities through Erasmus+K107 programme: Faculty of Biology M.V. Lomonosov Moscow State University, Rusia
2007 – on-going Supervisor of doctoral students on Graduate School (Karstology (III. level), University of Nova Gorica, Slovenia (http://www.ung.si/en/study/graduate-school/study/3KR/supervisors/)
2006 – on-going Teaching consists of class work, laboratory work, field practice and group exercises for graduate and postgraduate students at the Department of Biology, Faculty of Science, University of Zagreb.

ORGANISATION OF SCIENTIFIC MEETINGS

member of the scientific and organising committee of three national and one international meetings.

INSTITUTIONAL RESPONSIBILITIES

2014 – 2018 Member of the Board of the Doctoral study on Department of Biology, Faculty of Science, University of Zagreb, Croatia
2012 – 2015 Head of the Graduate Study Programme - Ecology and Nature Conservation on Department of Biology, Faculty of Science, University of Zagreb, Croatia
2012 – 2015 Member of the admission commission on Graduate Studies at the Department of Biology, Faculty of Science, University of Zagreb, Croatia

RESEARCH INTEREST: Crustaceology, Aquatic Ecology, Groundwater Biology, Water Management, Environmental Sciences, Ecotoxicology

OTHER SIGNIFICANT ACADEMIC ACHIEVEMENTS

(i) Scientific work within projects: 4 EU projects integration of Natura 2000 (2006-2016); (ii) actively participate in Scientific Societies: the International Society of Subterranean Biology - general secretary (2012-2016), Vice-president of Croatian Ecological Society (2018-ongoing); (iii) Reviewer in five scientific Journals (WoS); (iv) Reviewer of competitive scientific projects, etc.

PAPERS: 54 peer reviewed original scientific publications; 3 chapters in scientific books; 358 citations (Scopus), h-index 12; 81 lectures and posters at scientific conferences.

Dr. sc. Stefano Taiti

EDUCATION

April 1977: Degree of Doctor in Biological Sciences, University of Florence, Italy.

PROFESSIONAL EXPERIENCE

1980-1982: Researcher in Zoology, Ministery of Culture and Environment, Italian Republic.
1982-2001: Researcher of the Italian National Council of Research, Centro di Studio per la Faunistica ed Ecologia Tropicali, Florence, Italy.
2002-2017: Senior Researcher of the Italian National Council of Research, Istituto per lo Studio degli Ecosistemi, Florence, Italy.
2005-2015: Contract Professor, Course of Zoogeography, Faculty of Natural Sciences, University of Florence.
2017-present: Associate Researcher of the Italian National Council of Research, Istituto di Ricerca sugli Ecosistemi Terrestri, Florence, Italy.

RESEARCH INTERESTS

Systematics, phylogeny, biogeography, functional morphology and ecology of terrestrial isopods (Crustacea, Oniscidea), particularly from tropical and Mediterranean regions.

CONGRESS ORGANIZER

1) II International Symposium on the Biology of Terrestrial Isopods, Urbino, Italy, 10-12 Sept. 1986.
2) XI International Symposium of Biospeleology, Florence, Italy, 28 Aug.-2 Sept. 1994.
3) V International Symposium on the Biology of Terrestrial Isopods, Heraklion, Crete, Greece, 19-23 May 2001.
4) 8th International Symposium of Terrestrial Isopod Biology, Bled, Slovenia, 19-23 June 2011.
5) "Biology and Biodiversity of Peracarida Session" , Congress of The Crustacean Society (TCS) & the Latin American Association of Carcinology (ALCARCINUS), San José, Costa Rica, 7-11 July 2013.
6) 10th International Symposium of Terrestrial Isopod Biology, Budapest, Hungary, 27-30 August 2017.

EDITORIAL ACTIVITY

- Co-Editor of the eight volumes on the biology of terrestrial Isopoda (Crustacea, Oniscidea):
- Editor-in-Chief of the international journal TROPICAL ZOOLOGY published by the Istituto di Ricerca sugli Ecosistemi Terrestri, CNR, Florence, Italy.
- Co-editor for the Isopoda Oniscidea of the World Register of Marine Species (WoRMS).

CONGRESS COMMUNICATIONS and SCIENTIFIC PUBLICATIONS

About 80 contributions to international congresses, symposia and workshops and 175 scientific publications on the biology of terrestrial Isopoda mainly in international journals.

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University of Zagreb
Faculty of Science
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Doctoral thesis

MORPHOLOGY AND MOLECULAR PHYLOGENY OF THE CAVE DWELLING SUBGENUS *ILLYRIONETHES* VERHOEFF, 1927 (ISOPODA, TRICHONISCIDAE) IN THE DINARIC KARST

JANA BEDEK
Croatian Biospeleological Society, Demetrova 1, Zagreb

The subterranean southern European genus *Alpioniscus* consists of two subgenera: *Alpioniscus* s.s. and *Illyrionethes*, with 33 species described. In Dinaric Karst, 13 nominal and 12 putative undescribed troglobiotic *Illyrionethes* have been recorded. The aim of the study was to confirm the existence of the nominal and undescribed species of the Dinaric *Illyrionethes*, bring insights into the phylogenetic groups, their mutual relationships, distributions and differential characters of the species. The molecular analyses using two mtDNA (16S rRNA and COI) and a nuclear gene (H3) fragments have been performed, as well as detailed taxonomical study on all nominal and seven undescribed Dinaric species. The results confirmed the validity of 12 out of 13 nominal and all undescribed species. The nominal species, *A. bosniensis* is considered to be a junior synonym of *A. heroldi*, based on molecular and morphological analyses. Seven new species have been described: *A. iapodicus*, *A. hirci*, *A. velebiticus*, *A. lossinii*, *A. drazinai*, *A. mandalinae,* and *A. busljetai*. As a result, 19 nominal species of *Illyrionethes* are currently known from the Dinaric Karst. They grouped into three distinct lineages: *strasseri*-, *heroldi*- and *magnus*-lineage. All lineages follow a northwest-southeast direction of the Dinaric Karst and have overlapping distributions. The *strasseri*-lineage was thoroughly sampled and highly supported by all phylogenetic methods employed, so a detailed morphological analysis was performed. Novel morphological characters, specific body part ratios (length and hump ending point of male pereopod 7 carpus; length and concavity turning point male pleopod 1 exopod), are proposed for future species identifications.

Keywords: 16S/cave fauna/COI/Histone 3/new species/Oniscidea/terrestrial isopods/Trichoniscinae

(198 pages, 34 figures, 10 tables, 144 references, original in English)

The Thesis is deposited in University Library in Zagreb, Ul. Hrvatske bratske zajednice 4, Zagreb.

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Doktorski rad

MORFOLOGIJA I MOLEKULARNA FILOGENIJA TROGLOBIONTSKOG PODRODA *ILLYRIONETHES* VERHOEFF, 1927 (ISOPODA, TRICHONISCIDAE) U DINARSKOM KRŠU

JANA BEDEK
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Podzemni južnoeuropski rod *Alpioniscus* se sastoji od dva podroda: *Alpioniscus* s.s. i *Illyrionethes* s 33 opisane vrste. Na Dinarskom kršu je bilo zabilježeno ukupno 13 nominalnih te 12 pretpostavljenih neopisanih troglobiontnih vrsta podroda *Illyrionethes*. Cilj ovog istraživanja bio je potvrditi nominalne i neopisane vrste dinarskih svojti podroda *Illyrionethes*, donijeti nove spoznaje o filogenetskim grupama, njihovim međusobnim odnosima, arealima i ključnim taksonomskim obilježjima za razlučivanje pojedinih vrsta unutar ovog podroda. Provedene su detaljne taksonomske analize te molekularne analize odsječaka gena podrijetlom iz mitohondrijske DNK (citokrom oksidaza podjedinica I–COI i veća podjedinica ribosomalne RNK–16S) te iz jezgrine DNA (histon H3). Analizirane su sve nominalne te sedam neopisanih vrsta. Rezultati su potvrdili 12 od 13 nominalnih i sve analizirane neopisane vrste. Molekularnom i takosnomskom analizom je utvrđeno kako je nominalna svojta *A. bosniensis* sinonim imena *A. heroldi*. Opisano je sedam novih vrsta: *A. iapodicus*, *A. hirci*, *A. velebiticus*, *A. lossinii*, *A. drazinai*, *A. mandalinae* i *A. busljetai*. Rezultat istraživanja je 19 nominalnih vrsta trenutno poznatih s Dinarskog krša. Grupirale su se u tri filogenetske grupe: *strasseri*-, *heroldi*- i *magnus*-grupa. Areali sve tri grupe se preklapaju te prate sjeverozapadno-jugoistočan smjer pružanja Dinarida. Najpotpunije su prikupljene jedinke *strasseri*-grupe, čiji su međusobni odnosi značajno podržani filogenetskim metodama. Stoga su na jedinkama ove linije provedena detaljna taksonomska istraživanja. Nove morfološke značajke, poput specifičnih omjera dijelova tijela (duljina karpusa i duljina grbe karpusa sedme nožice mužjaka; duljina odsječka i duljina stacionarne točke konkavnosti vanjskog ruba vanjskog odsječka prvog para začane nožice), su predloženi za buduće taksonomsko određivanje vrsta.

Ključne riječi: 16S/špiljska fauna/COI/Histone 3/nove vrste/Oniscidea/kopneni jednakonožni rakovi/Trichoniscinae

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Ocjenjivači: Dr. sc. Tvrtko Dražina, Dr. sc. Helena Ćetković, Dr. sc. Maja Zagmajster

Sažetak

Podzemni južnoeuropski rod *Alpioniscus* se sastoji od dva podroda: *Alpioniscus* s.s. i *Illyrionethes*. Podrod *Alpioniscus* s.s. ima 13 zabilježenih vrsta, a rasprostranjen je na području talijanskih i francuskih Alpa te na južnom Balkanu u Grčkoj, Sjevernoj Makedoniji, Kosovu i Albaniji. Podrod *Illyrionethes* je poznat iz sjeveroistočne Španjolske s jednom vrstom, iz Sardinije sa šest vrsta i s Dinarskog krša. Prethodnim istraživanjima na Dinarskom kršu je bilo zabilježeno ukupno 13 poznatih te 12 pretpostavljenih, neopisanih vrsta. Sve poznate vrste roda *Alpioniscus* su podzemne, većina su troglobionti, osim jedne endogejske sardinijske vrste *A. thanit* te stigobionskih vrsta *A. stochi*, *A. sideralis* i *A. kuenhi.*

Cilj ove studije bio je potvrditi poznate i neopisane vrste dinarskih vrsta podroda *Illyrionethes*, donijeti nove spoznaje o filogenetskim grupama, njihovim međusobnim odnosima, arealima i ključnim taksonomskim obilježjima za razlučivanje pojedinih vrsta unutar ovog podroda.

Pregledane su sve dostupne jedinke roda *Alpioniscus* s Dinarskog krša iz svih dostupnih zbirki, a prikupljene su i dodatne jedinke na području rasprostranjenosti. Poznate vrste su sakupljane iz tipskih lokaliteta, ukoliko je to bilo moguće, odnosno najbližeg poznatog lokaliteta tipskom lokalitetu. Dodatno su sakupljene jedinke poznatih vrsta iz drugih populacija. Ukupno je analizirano 5 070 jedinki.

Provedene su detaljne molekularne analize na 64 jedinke svih poznatih i sedam neopisanih vrsta. Analizirani su odsječci gena podrijetlom iz mitohondrijske DNK (citokrom oksidaza podjedinica I–COI i veća podjedinica ribosomalne RNK–16S) te iz jezgrine DNK (histon H3). Filogenetski odnosi analizirani su metodama „Maximum Likelihood“ (ML) te „Bayesian inference“ (BI), dok je vrijeme odvajanja filogenetskih grupa procijenjeno temeljem 16S odsječka gena, programskim paketom BEAST. Vrste *Spelaeonethes mancinii* i *Oritoniscus flavus* su uključene u filogenetsku analizu u svojstvu vanjskih grupa.

Za taksonomske analize pojedine jedinke mužjaka su secirane i pripremljene kao mikropreparati u Hoyerovom mediju. Za određivanje vrsta, opise i detaljne taksonomske analize na mikropreparat je položeno cijelo tijelo i tjelesni privjesci: prvi i drugi par ticala, privjesci usnog aparata, svih sedam pari nožica te svih pet pari začanih nožica i genitalna papila. Sve utvrđene vrste su ilustrirane

i opisane, a nove vrste su imenovane. Ilustracije su izrađene temeljem fotografija ili upotrebom optičkog pomagala (camera lucida). Terminologija korištena u opisima vrsta se oslanja uglavnom na Vandela (1960, 1962).

Rezultati su potvrdili 12 od 13 poznatih i svih pet analiziranih neopisanih vrsta. I molekularnom i taksonomskom analizom je utvrđeno da je naziv svojte *A. bosniensis* sinonim vrste *A. heroldi*. Imenovano je i opisano sedam novih vrsta: *A. iapodicus*, *A. hirci*, *A. velebiticus*, *A. lossinii*, *A. drazinai*, *A. mandalinae* i *A. busljetai*. Trenutno je ukupno poznato 19 vrsta s Dinarskog krša.

Dinarske vrste roda *Alpioniscus* su se grupirale u tri filogenetske grupe: *strasseri*-, *heroldi*- i *magnus*-grupa. Devet vrsta pripada *heroldi*-grupi: *A. heroldi, A. haasi, A. kratochvili, A. absoloni, A. trogirensis*, *A. verhoeffi*, *A. tuberculatus, A. herzegowinensis* i *A. busljetai*. Šest vrsta pripada *strasseri*-grupi: *A. strasseri; A. balthasari, A. christiani, A. hirci* i *A. velebiticus*. Četiri vrste pripadaju *magnus*-grupi: *A. magnus, A. lossinii, A. drazinai,* i *A. mandalinae*. Filogenetska *magnus*-grupa je dobro podržana analizom odsječka gena 16S, dok zajedničkom analizom odsječaka gena 16S i H3 nije potvrđena te status nije pouzdan. Filogenetske grupe su se odvojile prije oko 10 do 9 milijuna godina, dok su se vrste odvojile prije oko 10 do 2 milijuna godina.

Areali sve tri grupe se preklapaju te prate sjeverozapadno-jugoistočan smjer pružanja Dinarida. Međusobni odnosi su definirani s najvećom značajnosti kod *strasseri*-grupe. Stoga su na njoj provedena detaljna taksonomska istraživanja. Nove morfološke značajke, poput specifičnih omjera dijelova tijela (duljina karpusa i duljina grbe karpusa sedme nožice mužjaka; duljina odsječka i duljina stacionarne točke konkavnosti vanjskog ruba vanjskog odsječka prvog para začane nožice), su predloženi za buduće taksonomsko određivanje vrsta.

Morfološki se *strasseri*-grupa razlikuje od *heroldi*- i *magnus*-grupe po obliku vanjskog odsječka prvog para začane nožice, čiji je vanjski rub duboko konkavan, za razliku od slabo ili ne konkavnog vanjskog ruba. Morfološka analiza nije utvrdila nikakve razlike između vrsta *magnus*- i *heroldi*-grupa. Dijagnostičke morfološke značajke s najznačajnijim specifičnim diskriminativnim vrijednostima su: i) oblik vanjskog ruba vanjskog odsječka prvog para začane nožice mužjaka, ii) oblik i pozicija sternalnog režnja merusa sedme noge mužjaka te iii) prisutnost, duljina i oblik tergalne grbe karpusa sedme noge mužjaka.

Table of Contents

INTRODUCTION

The subterranean biodiversity in the Dinaric Karst

The Dinaric Karst is predominantly a mountain area with remarkable caves, sinking streams, and other karst features. It stretches in the so-called *Dinaric direction* from the Trieste area, Italy in the north-west, through parts of Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro to the Prokletije Mt., Albania in the south-east. It is bordered by the Adriatic Sea on the south-west and Pannonian Basin on the north-east, the south-east Alps on the north-west and Taurid Mts. on the south-east. It is approximately 650 km long and 150 km wide, and covers some 60 000 km^2 in total, forming the most extensive continuous karst landscape in Europe (Mihevc et al. 2010; Zupan Hajna 2019)(Figure 1).

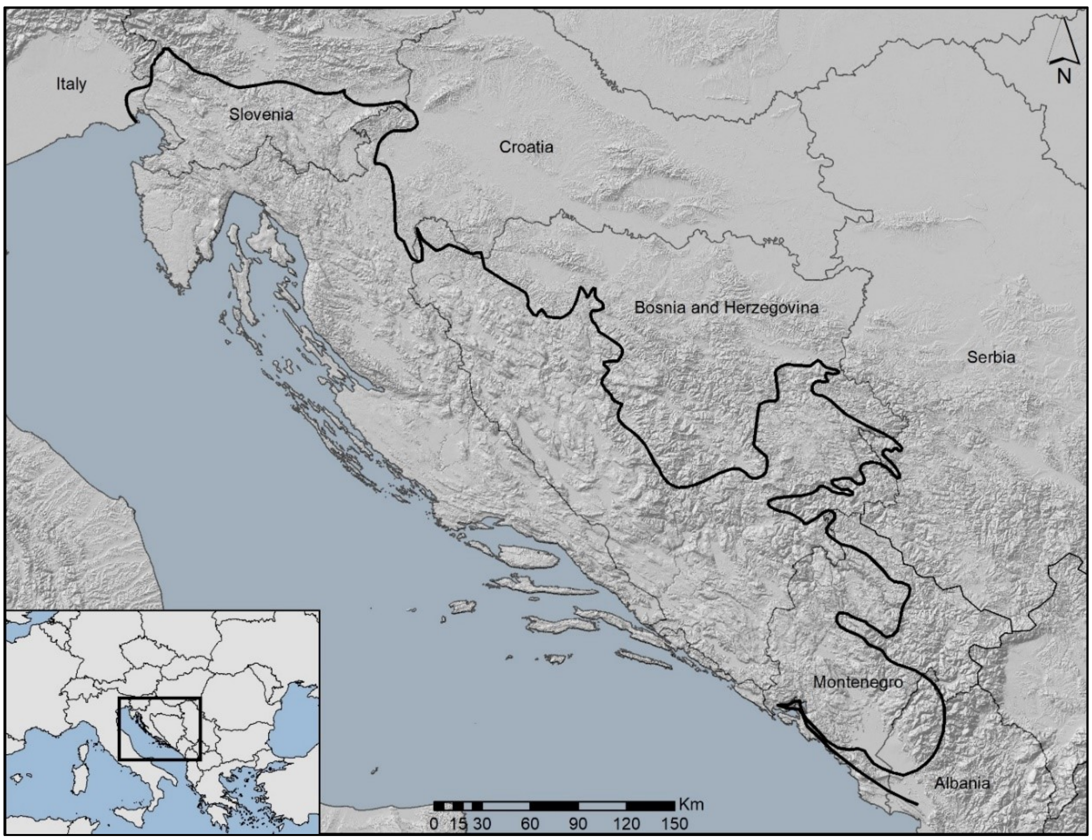

Figure 1. Map of the Dinaric Karst (border indicated with a thick line), after Bonnaci et al. (2008), adapted.

Dinarides are considered to be a hotspot of subterranean biodiversity (Culver and Sket 2000; Sket et al. 2004; Sket 2012; Deharveng et al. 2012; Zagmajster et al. 2014; Simičević 2017), with nearly

1000 out of the total 7000 world subterranean species (Sket 2012; Deharveng et al. 2019). Moreover, Dinaric Karst is home of peculiar representatives unknown from any other regions, such as the sponge *Eunapius subterraneus* Sket and Velikonja, 1986; the hydrozoan *Velkovrhia enigmatica* Matjašič and Sket, 1971; bivalves *Congeria* spp.; the polychaete *Marifugia cavatica* Absolon and Hrabe, 1930; the only flying blind dipteran *Troglocladius hajdi* Andersen, Baranov and Hagenlund, 2016; and the only European cave vertebrate, the olm *Proteus anguinus* Laurenti, 1768 (Sket 2012). Such high subterranean biodiversity in the Dinaric Karst is related to their complex geological history and intensive karstification which enabled multiple colonisations of the subterranean realm (Bilandžija et al. 2013).

Due to well-expressed karst phenomena, geographic position, geological history and environmental heterogeneity, the Dinaric Karst is of extreme interest for speleobiological studies which began in the first half of 19th century (Sket 2012). Nevertheless, the subterranean biodiversity remains mostly understudied, as indicated by the number of new taxa described every year (e.g., Hlaváč et al. 2019; Lukić et al. 2018; Delić et al. 2017b; Pavlek and Ribera 2017; Andersen et al. 2016). For example, for Croatia alone, 12 and nine new taxa were described in 2017 and 2018, respectively (Bregović 2018). Some species and genera have wide distributions within the Dinaric Karst [holodinaric distribution (*sensu* Sket 2012)], but they rarely extend beyond its border. Merodinaric distribution patterns (*sensu* Sket 2012) of genera or species are usually characterized by bipolarity with north-western and south-eastern elements, while some demonstrate paralittoral distribution patterns (*sensu* Sket 2012). Most species and subspecies, but also some genera, exhibit very small distribution areas, and very often they are known only from their type localities. Even though no synthesis is available, it is safe to conclude that the endemism of troglobionts within the Dinaric Karst is high. The average is of about 40 to 60% of species endemic to each state in the area, which would be much higher in natural biogeographic provinces (Sket 1994; 2012).

High levels of habitat fragmentation in subterranean ecosystems often lead to lineage isolations and potentially speciations (Gorički and Trontelj 2006; Trontelj et al. 2007; Zakšek et al. 2007; Trontelj et al. 2009; Prevorčnik et al. 2010). However, convergent adaptations, due to high homogeneity of cave environment, can result in cryptic species (Lefébure et al. 2006; Finston et al. 2007; Zakšek et al. 2009; Baratti et al. 2010; Bilandžija et al. 2013; Delić et al. 2017a; 2017b;).

Therefore, molecular studies are often essential to clarify phylogenetic relationships and biogeography in troglobiotic taxa, even fundamental in Dinaric Karst where complex palaeogeography makes the interpretation of evolutionary history very complicated. Subterranean morpho-species can consist of deeply divergent lineages (Bilandžija et al. 2013; Weigand et al. 2013; Delić et al. 2017a). Stygobiotic lineages can be widely distributed with ranges up to 400 km (Baratti et al. 2010; Jugović et al. 2012), but more often they are highly stenoendemic (Zakšek et al. 2009; Bilandžija et al. 2013; Delić et al. 2017a; 2017b). Molecular analyses of Dinaric terrestrial troglobionts did not include any widespread or holodinaric taxon up to now, and the widest ranges are mostly less than 50 km in diameter (Weigand et al. 2013; Andersen et al. 2016; Polak et al. 2016; Njunjić et al. 2016; Njunjić et al. 2017; Pavlek and Ribera 2017; Njunjić et al. 2018; Lukić et al. 2018; Bregović et al. 2019).

Suborder Oniscidea with an emphasis of the family Trichoniscidae

To date, more than 10 000 species have been described within the order Isopoda (Boyko et al. 2008), the most diversified order of Peracarida superorder. Oniscidea, the largest of ten Isopoda suborders, encompasses more than 3 700 species (Boyko et al. 2008; Sfenthourakis and Taiti 2015). They are convincingly the most successful colonizers of terrestrial habitats within Crustacea, occupying various habitats and most areas of the world (Sfenthourakis and Taiti 2015). The supralittoral genus *Ligia* Fabricius, 1798 is considered as the closest present-day relative of a marine ancestor (Broly et al. 2013). The amphibious and aquatic species, either freshwater or salt lake ones, do not have a freshwater or marine origin but have secondarily returned to live in aquatic environments (Taiti and Xue 2012). The opposite extreme is several desert species, e.g. *Hemilepistus reaumurii* (Milne-Edwards, 1840), which digs burrows in the sand and has a complex social behaviour (Linsenmair 1975). Oniscidea can reach the altitudes of 4800 m in Himalaya, and there are around 140 species observed at or above the altitudes of 2200 m (Beron 1997). The majority of isopods are typical members of the soil macrofauna community. Moreover, as primary decomposers, they play an essential role in the process of soil formation (e.g., Wolters and Ekschmitt 1997). Around 10% of species are troglobionts (Deharveng and Bedos 2018), occupying subterranean habitats with very high abundance. The only terrestrial Oniscidea free areas in the world are the poles and very high elevations (Sfenthourakis and Taiti 2015).

The global scale analysis of Oniscidea distribution data are still not available, but some general rules were obtained from available data, mainly from the World catalog of terrestrial isopods (Isopoda: Oniscidea) (Schmalfuss 2003). Latitudinal gradients of species richness show peaks in both northern and southern mid-latitudes. Terrestrial isopods do not seem to follow the Rapoport's rule since the range of distributions is not related to latitude (Sfenthourakis and Hornung 2018). Isopod richness is highly correlated with geographical and landscape complexity and environmental heterogeneity. Circum-Mediterranean regions exhibit the highest biodiversity of Oniscidea, together with some tropical insular areas and regions with Mediterranean-Type Ecosystems (Sfenthourakis and Taiti 2015; Sfenthourakis and Hornung 2018). At the European level, the contribution of endemics dominates in the south, with peaks in Iberian, Apennine and Balkan peninsulas (Sfenthourakis and Hornung 2018).

Oniscidea is currently considered to be a monophyletic taxon, even though recent molecular analyses question this hypothesis, whereas *Ligia oceanica* (Linnaeus, 1767) did not cluster with the rest of Oniscidea species (Lins et al. 2017; Hua et al. 2018; Zou et al. 2018). Five sections of the suborder are generally accepted: Diplocheta Vandel, 1957, Tylida Erhard, 1995, Microcheta Schmalfuss, 1989, Synocheta Legrand, 1946, and Crinocheta Legrand, 1946. The molecular phylogeny of families and genera are still missing, and present-day relationships hypothesis are based on morphology alone (e.g., Schmidt 2008). Several phylogenetic studies on epigean and cave Oniscidea were performed thus far (Rivera et al. 2002; Klossa-Kilia et al. 2006; Montesanto et al. 2007; Cooper et al. 2008; Parmakelis et al. 2008; Poulakakis and Sfenthourakis 2008; Karasawa and Honda 2012; Kamilari et al. 2014; Lee et al. 2014; Raupach et al. 2014; Zimmermann et al. 2015; Zimmermann et al. 2018; Dimitriou et al. 2018), and only one focused on Synocheta taxa, namely Sardinian *Illyrionethes* (Taiti et al. 2018). They showed that traditional taxonomic characters should be revised in some cases (Klossa-Kilia et al. 2006; Parmakelis et al. 2008; Lee et al. 2014; Zimmermann et al. 2018; Dimitriou et al. 2018) whereas in others they confirmed that the current taxonomy based on rather small morphological differences is correct (Zimmermann et al. 2015). Estimations of divergence times within Oniscidea has seldom been analysed, and the only available estimations of splits are between *Armadillidium* Brandt, 1833 species (~ 10 MYA), *Porcellio dilatatus* Brandt, 1833 subspecies (~5 MYA) and *Orthometopon* Verhoeff, 1917 Greek populations (9-5 MYA) (Poulakakis and Sfenthourakis 2008; Becking et al. 2017; Dimitriou et al. 2018).

With 87 genera and ~500 species, the Trichoniscidae G. O. Sars, 1899 is within Oniscidea the second and third largest family, respectively (Boyko et al. 2008; Sfenthourakis and Taiti 2015). Trichoniscidae, as part of the section Synochaeta, did not develop pleopodal lungs. They are considered to be more depending on the relative air humidity, ie. less adapted to terrestrial habitats among Oniscidea. Therefore, it is not surprising that about 70% of known oniscidean troglobionts belong to the family Trichoniscidae (Taiti 2004). Altogether 20 genera of Trichoniscidae are recorded within the Dinaric Karst, seven of them being endemic: *Titanethes* Schioedte, 1849, *Cyphonethes* Verhoeff, 1926, *Stylohylea* Verhoeff, 1930, *Protonethes* Absolon & Strouhal, 1932, *Cyphopleon* Frankenberger, 1940, *Strouhaloniscellus* Tabacaru, 1993, and *Cetinjella* Karaman & Horvatović, 2018. Without the results of this study, 26 troglobiotic species in nine genera of Trichoniscidae were known (Karaman, 1966; Schmalfuss, 2003; Karaman and Horvatović 2018; Boyko et al. 2008).

The family Trichoniscidae consists of four subfamilies, i.e. Trichoniscinae G. O. Sars, 1899, Haplophthalminae Verhoeff, 1908, Buddelundiellinae Verhoeff, 1930, and Thaumatoniscellinae Tabacaru, 1973. The classification of the family is mainly based on the male copulatory apparatus and habitus (Tabacaru 1993; 1996). At present the subfamily Trichniscinae is divided into six tribes: Trichoniscini Sars, 1899, Typhlotricholigioidini Rioja, 1953; Spelaeonethini Schmölzer, 1965; Trichoniscoidini Schmölzer, 1965; Oritoniscini Tabacaru, 1993 and Androniscini Tabacaru, 1993.

Alpioniscus in the Dinaric Karst

The genus Alpioniscus belongs to the tribe Spelaeonethini of subfamily Trichoniscinae (Tabacaru 1996). The first *Alpioniscus* species was described from the Italian Alps as *Titanethes feneriensis* Parona, 1880. The genus *Alpioniscus* was established by Racovitza (1908) for the species *Trichoniscus* (*Alpioniscus*) *dispersus* (Racovitza, 1907) from the French Alps, now considered to be a junior synonym of *A. feneriensis* (Parona, 1880). The second described species was from Italy as well (Sardinia), named *Titanethes fragilis* Budde-Lund, 1909, placed in the genus *Alpioniscus* by Arcangeli (1940) and in the subgenus *Illyrionethes* by Vandel (1946). The genus *Illyrionethes* was erected by Verhoeff (1927) for the new species *Illyrionethes strasseri* from a cave near Trieste (Italy). Kesselýak (1930) synonymized *Illyrionethes* with the genus *Alpioniscus*, while Vandel

(1946) considered *Alpioniscus* s.s. and *Illyrionethes* as two subgenera of the genus *Alpioniscus*, which is the present taxonomic classification.

Both subgenera of *Alpioniscus* have disjunct distributions. *Alpioniscus* s.s. is distributed in south-east France and western Italian Alps with single species and south Balkans with 13 species (Schmalfuss 2003; Andreev 2013a; Andreev 2013b). *Illyrionethes* is known from north-east Spain with single species (Cruz and Dalens 1989), Sardinia (Italy) with six species (Taiti et al. 2018) and Dinaric Karst. Prior to the results of this study, in the Dinaric Karst 13 nominal and 12 putative undescribed species have been recognized (Schmalfuss 2003, Bedek and Taiti 2011; Horvatović, 2014). The distribution areas of both subgenera do not overlap.

All *Alpioniscus* species are adapted to the underground environment, with the majority being terrestrial troglobionts. The exceptions are some Sardinian species: the endogean *A. thanit* Taiti & Argano, 2009, and the stygobiotic *A. stochi* Taiti & Argano, 2018, *A. sideralis* Taiti & Argano, 2018, and *A. kuenhi* (Schmalfuss 2005) (Taiti and Argano 2009; Taiti et al. 2018).

In the Dinaric Karst, the majority of research was conducted in the first half of the 20th century, prior to the Second World War. The complete history of *Alpioniscus* research is not possible to analyse since many published data in (old) literature lack collection dates and/or legators. Here is presented only a part of available historical data, selected by the following criteria: type material collections, the oldest collections, and the most comprehensive research. The first known *Alpioniscus* specimens were collected by the Austrian biologist Joseph Erber in caves in the surrounding of the river Neretva in 1861. These were later described as *Illyrionethes verheoffi* by the Austrian isopodologist Hans Strouhal (1938). Different researchers collected *Alpioniscus* at the end of 19th and beginning of the 20th century. The archaeologist and speleologist from Trieste Ludwig Karl Moser collected *A. strasseri* in Belinca jama in Slovenia in 1885 (Strouhal 1938; 1940). In 1902 the Austrian entomologist Gustav Paganetti-Hummler collected *A. heroldi* in the cave Grabovica near Trebinje in Herzegovina (Strouhal 1938). The director of the Croatian Natural History Museum August Langhoffer collected *Alpioniscus* sp. in Medina pećina near Prušić in Lika region (Bedek et al. 2011). The Czech coleopterologist Joseph Klimesch in 1913 collected *Alpioniscus balthasari* in the surrounding of the town Sinj in Dalmatia (Strouhal 1938). A mammalogist from Vienna, Otto Wettstein, explored caves on the island of Brač in 1912 in an expedition organized by the biologist Prof. Dr. Franz Werner, where he collected *Alpioniscus* *magnus* (Strouhal 1939b). The Dalmatian cave fauna was investigated by Umberto Girometta, a school teacher and speleologist from Split, and his students from 1912 to 1914, where they collected *Alpioniscus balthasari* (Strouhal 1939b). The Czech biologist Karel Absolon, one of the most famous explorers of Dinaric caves, assembled the great collection *Biospeleologica balcanica,* with the contribution of many other researchers besides Absolon. *Alpioniscus* material was collected from 1903 to 1930, mainly in Herzegovina (surroundings of Trebinje, Popovo polje, Bihovo, Nevesinje, Gacko, Visočica, Jablanica) as well as near Livno in Bosnia. Additionally, important material was collected in Dalmatia, on the island of Brač and the mainland (surroundings of Cetina, Sinj, Šibenik, mountains Mosor and Moseć), and in Istria and Gorski kotar. In Italy *Alpioniscus* was collected from two caves near Trieste. Strouhal identified the Oniscidea from that collection, and published several papers including the description of *A. absoloni* and it's two subspecies (Strouhal 1939a; 1939c; 1939d; 1939b; Bedek et al. 2011). The Macedonian crustaceologist Stanko Karaman collected *A. trogirensis* in 1924 in the surrounding of Trogir, Dalmatia (Buturović 1955a). In 1927 the diplopodologist Karl Strasser collected specimens from caves near Trieste and Sežana which were analysed by the German isopodologist Karl Verhoeff who described the new genus and species *Illyrionethes strasseri* (Verhoeff 1927). The same year, the German zoologist Fritz Haas collected *A. haasi* from the island of Korčula (Verhoeff 1931b). The Slovak isopodologist Zdeněk Frankenberger made a two-week-long fieldtrip in Dalmatia in June 1937 and described the species *Alpioniscus balthasari* (Frankenberger 1937). In 1939 the Czech arachnologist Josef Kratochvíl collected material in Bosnia near Tomislavgrad and Livno, including two new species, *A. bosniensis* and *A. tuberculatus* (Frankenberger 1939). In the sixties in Trieste surroundings the Italian arachnologist Fulvio Gasparo and the curator Giorgio Alberti collected isopods together with Strasser (Paoletti 1978). In 1978 the Austrian collembologist Erhard Christian collected the new species *A. christiani* in the island of Krk (Potočnik 1983). Altogether Verhoeff described four Dinaric *Illyrionethes* species (Verhoeff 1927; 1931a; 1931b), Frankenberger five (Frankenberger 1937; 1938; 1939), Strouhal two species and two subspecies (Strouhal 1938; 1939), Burutović (1955) and Potočnik (1983) one species each. After the formation of the Croatian Biospeleological Society in 1996, numerous cavers and biologists collected *Alpioniscus*, mainly in Croatia (Bedek et al. 2011), as well as in the rest of Dinarides. That material is the basis of the present study.

Species distributions differ in size. Species with largest ranges are *A. strasseri* (Verhoeff, 1927), from Trieste (Italy), Istria (Croatia and Slovenia), the island of Cres and Gorski Kotar (Croatia), *A. balthasari* (Frankenberger, 1937) in whole middle Dalmatia (Croatia), Livanjsko polje and Duvanjsko polje (Bosnia and Herzegovina), *A. heroldi* (Verhoeff, 1931) around the towns of Bileća and Trebinje, Popovo polje and Dabarsko polje, mountains Kubaš Planina, Sitnica Planina (Bosnia and Herzegovina), and *A. absoloni* (Strouhal, 1939) around the towns of Bileća and Jablanica, Nevesinjsko polje and mountain Visočica Planina (Bosnia and Herzegovina). The species *A. bosniensis* (Frankenberger, 1939) has a disjunct distribution in Duvanjsko polje, in Široki Brijeg area (Bosnia and Herzegovina) and Biokovo mountain (Croatia). All other species have very restricted distributions: *A. tuberculatus* (Frankenberger, 1939) in the town of Livno (Bosnia and Herzegovina), *A. trogirensis* Buturović, 1955 around the town of Trogir (Croatia), *A. verhoeffi* (Strouhal, 1938) in the valley of Neretva river (Bosnia and Herzegovina or Croatia), *A. herezgowinensis* (Verhoeff, 1931) around the town of Trebinje (Bosnia and Herzegovina), *A. haasi* (Verhoeff, 1931) from the island of Korčula and Pelješac peninsula (Croatia) and some island endemics, i.e. *A. christiani* Potočnik, 1983 from the island of Krk, *A. magnus* (Frankenberger, 1938) from the island of Brač and *A. kratochvili* (Frankenberger, 1938) from the island of Hvar (Arcangeli 1932, Brian 1938; Buturović 1955a; Frankenberger 1937, 1939; Strouhal 1939a; 1939b; 1939c; 1939d; Vandel 1946; Verhoeff 1927; 1929; 1931b; 1938).

Morphological characteristics of *Illyrionethes*

In the Dinaric Karst only the subgenus *Illyrionethes* is present. The two subgenera of *Alpioniscus*, *Alpioniscus* s.s. and *Illyrionethes,* differ in the relative length of the proximal and distal article of the endopod of the male pleopod 2. In *Illyrionethes* the proximal article is distinctly longer than the distal one, while in *Alpioniscus* s.s both articles are subequal in length (Tabacaru, 1996). All nominal species fit this classification, except the Catalonian species *Alpioniscus escolai* Cruz & Dalens, 1989 which needs a taxonomic revision due to some morphological differences (Tabacaru 1996).

Morphological differences between species of *Illyrionethes* are very small and based on male secondary sexual characters in most cases. Few attempts to understand relationships among Dinaric *Illyrionethes* species have been made on the basis of morphological analyses alone (Frankenberger & Strouhal, 1940; Buturović, 1957; Bedek & Taiti, 2011; Horvatović, 2014). The original descriptions of nominal Dinaric *Illyrionethes* species are very concise. The following description of *Illyrionethes* is based on Catalonian, Sardinian and Dinaric species, exclusively from available data from the literature.

Illyrionethes species vary in size, and the smallest species is the Catalonian *A. escolai* (♂≤3 mm, ♀≤2,8 mm) (Cruz and Dalens 1989). Sardinian species vary from the smallest *A. stochi* Taiti & Argano, 2018 (♂, ♀≤ 4,5 mm) to the largest *A. fragilis* (♂≤9 mm, ♀≤14 mm), which is the largest known *Illyrionethes* (Taiti et al. 2018). Dinaric *Illyrionethes* vary from *A. trogirensis* (♂≤3 mm, ♀≤4 mm) to *A. bosniensis* (♂≤11 mm, ♀≤12 mm) (Frankenberger 1939; Buturović 1955).

All *Illyrionethes* species are unpigmented and without eyes, nevertheless their ecological preferences. The majority of species have smooth dorsum, and the exceptions are *A. fragilis, A. thanit, A. tuberculatus,* and *A. absoloni* with more or less strongly granulated tergites. Pleon epimerae are reduced, as in all Trichoniscinae species; subsequently, pleon is narrower than pereon (Taiti et al. 2018*;* Strouhal 1939a; Frankenberger 1939). The sides of the distal part of the telson are concave, and the apex is more or less broadly rounded, except in *A. sideralis* with a truncate and *A. escolai* with a narrowly rounded apex (Cruz and Dalens 1989; Taiti et al. 2018).

The antennula is made of three articles, and distal article is bearing a different number of aesthetascs on subapical and/or apical margin. The number of segments of the antennal flagellum varies from up to five (*A. escolai*) to up to 30 (*A. kuheni*), but the majority of species have around 10 segments (Cruz and Dalens 1989; Bedek and Taiti 2011; Taiti et al. 2018).

Buccal pieces are very different between terrestrial and aquatic species, due to different eating preferences in a different environment, but some similarities can be observed. Mandibles have one or two penicils in the right and three penicils in the left; the molar process is with none or one penicil in the right and none in the left. The outer branch of maxillula has 10 or 11 apical teeth, and one or two slender stalks; the inner branch has with three penicils. The apex of the maxilla is bilobate (except at *A. kuheni* and *A. stochi*), and setose (Taiti et al. 2018). The maxilliped shows the biggest difference between terrestrial and aquatic species, with the most considerable differences in the endite: in terrestrial species it is narrow, while in aquatic it is wide and quadrangular (Frankenberger 1938; Strouhal 1939c; Taiti et al. 2018).

The dactylar seta of the pereopods is in general bifid and setose, simple in some aquatic species. The uropod endopod is always shorter than exopod, and in the majority of species proximally inserted, with the exception of *A. kuheni* and *A. stochi* (Taiti et al. 2018).

Male characteristics are the main differential characters of *Illyrionethes* and in some cases the only ones. The male pereopod 7 ischium is always with straight sternal margin and bears one or more tooth-like processes or a hump (Cruz and Dalens 1989; Bedek and Taiti 2011; Taiti et al. 2018). The carpus of the male pereopod 7 is proximally enlarged in the Sardinian aquatic species, and with tergal hump in *A. strasseri, A. balthasari, A. christiani, A. magnus,* and *A. absoloni.* The genital papilla has a rounded apical part. The endopod of the male pleopod 1 is elongated and bearing a distinct apical seta. The shape of the male pleopod 1 exopod is species-specific. Basically, it is triangular, with more or less concave outer and/or inner margin, differing in the shape of ending point, relative length, and width. The male pleopod 2 endopod is longer than exopod, of two articles, where the proximal article is distinctly longer than the distal one, with the exception is *A. escolai* where it is distinctly longer than the proximal one. The distal article is bearing a terminal seta. The male pleopod 2 exopod is triangular (Cruz and Dalens 1989; Bedek and Taiti 2011; Taiti et al. 2018).

INDIVIDUAL PAPERS

1. Bedek J, Horvatović M, Karaman I (2017) A new troglobiotic species, *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. (Crustacea: Oniscidea: Trichoniscidae), from Lika region, Croatia. Natura Croatica 26: 205–214. https://doi.org/10.20302/NC.2017.26.17
2. Bedek J, Taiti S, Bilandžija H, Ristori E, Baratti M (2019) Molecular and taxonomic analyses in troglobiotic *Alpioniscus* (*Illyrionethes*) species from the Dinaric Karst (Isopoda: Trichoniscidae). Zoological Journal of the Linnean Society 187: 539–584. https://doi.org/10.1093/zoolinnean/zlz056
3. Bedek J, Gottstein S, Taiti S (2019) Taxonomy of *Alpioniscus* (*Illyrionethes*): *A. magnus* and three new species from the Dinaric Karst (Isopoda: Oniscidea: Trichoniscidae). Zootaxa 4657: 483–502. https://doi.org/10.11646/zootaxa.4657.3.4
4. Bedek J, Gottstein S, Taiti S (2019) A new species of *Alpioniscus* (*Illyrionethes*) from the Dinaric Karst (Isopoda, Oniscidea, Trichoniscidae). Subterranean Biology 32: 33–42. https://doi.org/10.3897/subtbiol.32.37509

Paper 1

Bedek J, Horvatović M, Karaman I (2017) A new troglobiotic species, *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. (Crustacea: Oniscidea: Trichoniscidae), from Lika region, Croatia. Natura Croatica 26: 205–214. https://doi.org/10.20302/NC.2017.26.17

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A NEW TROGLOBIOTIC SPECIES, *ALPIONISCUS (ILLYRIONETHES) IAPODICUS* N. SP. (CRUSTACEA: ONISCIDEA: TRICHONISCIDAE), FROM LIKA REGION, CROATIA

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Bedek, J., Horvatović, M. & Karaman, I. M.: A new troglobiotic species, *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. (Crustacea: Oniscidea: Trichoniscidae), from Lika region, Croatia. Nat. Croat., Vol. 26, No. 2, 205-214, 2017, Zagreb.

Alpioniscus (*Illyrionethes*) *iapodicus* n. sp. is described and illustrated. Representing the 14th nominal species of the subgenus *Illyrionethes* from the Dinaric karst, it is a troglobiotic species collected from the caves in the central part of the Lika region, Croatia. The new species belongs to the *strasseri* group. Morphological characters differentiating *A. iapodicus* from other *strasseri* group representatives are discussed.

Key words: Dinaric karst, Lika region, new species, *Alpioniscus*, Isopoda, terrestrial, Trichoniscidae, troglobiotic

Bedek, J., Horvatović, M. & Karaman, I. M.: Nova troglobiontska vrsta *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. (Crustacea: Oniscidea: Trichoniscidae) iz Like (Hrvatska). Nat. Croat., Vol. 26, No. 2, 205-214, 2017, Zagreb.

U radu se opisuje i ilustrira nova vrsta *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. Radi se o troglobiontnoj vrsti prikupljenoj u špiljama središnjeg dijela Like, i predstavlja četrnaestu nominalnu vrstu podroda *Illyrionethes* iz Dinarskog krša. Nova vrsta pripada grupi *strasseri*. Raspravlja se o morfološkim obilježjima koji razlikuju *A. iapodicus* od ostalih predstavnika te grupe.

Ključne riječi: Dinarski krš, Lika, nova vrsta, *Alpioniscus*, Isopoda, kopneni, Trichoniscidae, troglobiont

INTRODUCTION

The genus *Alpioniscus* includes two subgenera: *Alpioniscus* Racovitza, 1908, with 14 species, and *Illyrionethes* Verhoeff, 1927, with 16 species (Schmalfuss, 2003; Taiti & Argano, 2009; Andreev, 2013a,b). Both subgenera have disjunct ranges, and are distributed across karstic regions in the south of Europe. In all, 13 nominal species of the subgenus *Illyrionethes* have been recognized in the Dinaric Karst (Schmalfuss, 2003; Bedek *et al.*, 2011), while 11 putative species remain undescribed (Bedek & Taiti, 2011; Horvatović, 2014). All *Illyrionethes* species from the Dinaric karst are troglobionts. The new species was collected in 14 localities, underground caves, in the central part of the Lika region, Croatia; 11 of them are known today (Fig. 1). In the type locality, the cave Markov ponor, Lipovo polje, Donji Kosinj, Croatia, it was collected in the most distant channel, referred to as Kanal krivih brojeva (Channel of the wrong numbers) (Bakšić, 2008).

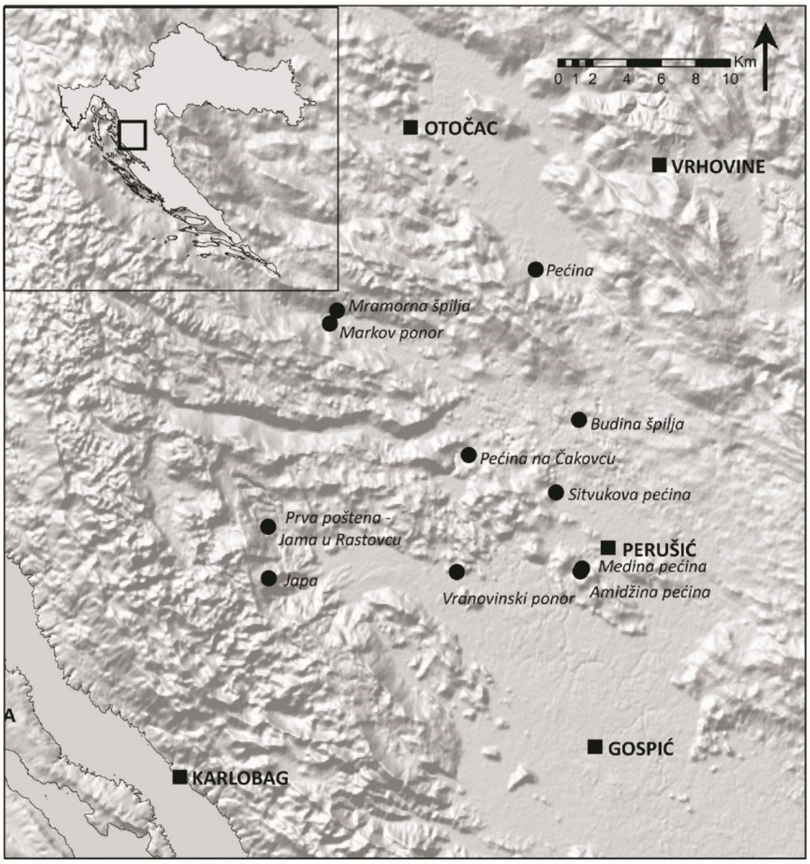

Fig. 1. Distribution of *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. (black circles).

MATERIAL AND METHODS

Specimens were hand collected with tweezers, fixed and stored in 75% ethanol with glycerol or 96% ethanol. Several specimens were dissected, and mounted for micropreparations in Hoyer's medium. Identifications are based on morphological characters indicated in the original descriptions. Specimens were examined under a Zeiss Stemi 2000-C and a Zeiss Primo Star microscope (Carl Zeiss, Jena, Germany). The micropreparations were photographed using Canon EOS 40D and EOS Utility software (Canon, Tokyo, Japan). The drawings were made based on the photographs, using CorelDRAW X8 (Corel Corporation, Ottawa, Canada). The examined material, species diagnosis and description, etymology and remarks are given. Terminology used in species description is mainly based on Vandel (1960, 1962). The locality coordinates are in the WGS84 coordinate system. The map was drawn using ArcMap 10.1 software and related basemap.

Abbreviations:

CBSSC	Croatian Biospeleological Society Collection, Zagreb, Croatia
CCC	Cave Cadastre of the Republic of Croatia, hosted by Croatian Agency for the Environment and Nature, Zagreb, Croatia (Croatian Agency for the Environment and Nature, 2017a)
CNHM	Croatian Natural History Museum, Crustacea Collection, Zagreb, Croatia
MZUF	Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia La Specola, Florence, Italy

SMNS Staatliches Museum für Naturkunde Stuttgart, Isopod Collection, Stuttgart, Germany

ZZDBE Zoological Collection of Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Serbia

TAXONOMY

Trichoniscidae

Trichoniscinae

Genus *Alpioniscus* Racovitza, 1908

Subgenus *Illyrionethes* Verhoeff, 1927

Alpioniscus iapodicus n. sp.

Synonymy: *Alpioniscus* (*Illyrionethes*) n. sp. 4: Horvatović, 2014, partim.

Type material. Holotype ♂ Croatia, Lika, Donji Kosinj, Lipovo polje, Markov ponor (CCC No. HR01480), 44,7653017089 °N, 15,1771778411 °E, 19.X.2011, leg. J. Bedek (CBSSC IT4109).

Paratypes: 6 ♂♂, 2 ♀♀, 2 juv. ibid. (CBSSC IT2479); 4 ♂♂, 4 ♀♀ ibid. (ZZDBE 1142); 2 ♂♂, 2 ♀♀ ibid. (MZUF 9763); ♂, ♀ Croatia, Lika, Ličko Lešće, Pećina, 44,7952856754 °N, 15,3279411137 °E, 22.IX.2005 leg. M. Pavlek (CBSSC IT3344); 1 juv. ibid. 7.II.2008 leg. R. Ozimec (CBSSC IT3347); ♂ Croatia, Lika, Donji Kosinj, Lipovo polje, Petranović Draga, Mramorna špilja, 44,772160231 °N, 15,1823031537 °E*, 30.V.1999 leg. R. Ozimec (CBSSC IT3367); ♂, 2 ♀♀ Croatia, Lika, Perušić, Studenci, Milkovići, Budina špilja (CCC No. HR01195), 44,716915063 °N, 15,3613735717° E, 24.VII.2007 leg. M. Pavlek (CBSSC IT3373); 2 ♂♂, ♀, 1 juv. ibid. 29.I.2011 leg. L. Đud (CBSSC IT3843); ♀ ibid. leg. H. Bilandžija (CBSSC IT3848); 2 juv. ibid. leg. P. Bregović (CBSSC IT3846); 2 ♂♂, ♀ ibid. 11.VI.2011 leg. B. Jalžić (CBSSC IT3374); 3 ♂♂, 1 juv. Croatia, Lika, Donji Kosinj, Mlakva, Javorinske drage, Pećina na Čakovcu (CCC No. HR01706) 44,6975593882 °N, 15,2808266387 °E, 2.V.2015 leg. B. Jalžić (CBSSC IT3765); 3 ♂♂, ♀ Croatia, Lika, Perušić, Sitvuki, Sitvukova pećina, 44,6786713198 °N, 15,3453423752 °E, 8.VIII.2014 leg. J. Bedek (CBSSC IT3383); ♂, ♀ Croatia, Lika, Perušić, Velika Plana, Rastovac, Prva poštena - Jama u Rastovcu (CCC No. HR00953), 44,6582649068 °N, 15,1343931909 °E, 2.VIII.2015 leg. D. Basara (CBSSC IT3921); ♀ Croatia, Lika, Perušić, Grabovača, Medina pećina, 44,6389475032 °N, 15,3651981516 °E, 14.VIII.1902, leg. A. Langhoffer (CNHM 653); 2 ♂♂, ♀, 2 juv. ibid. 30.XII.2011, leg. J. Bedek, M. Lukić (CBSSC IT2545); ♀ ibid. 12.V.2014, leg. K. Cindrić (CBSSC IT3381); ♀ ibid. 16.V.2014, leg. J. Bedek (CBSSC IT3907); 1 juv. ibid. 17.V.2014, leg. L. Kekelj (CBSSC IT3382); 3 ♂♂, 4 ♀♀, 4 juv. Croatia, Lika, Perušić, Grabovača, Amidžina pećina, 44,6373404989 °N, 15,3639653667 °E, 30.XII.2011, leg. J. Bedek, M. Lukić (CBSSC IT2546); ♀ ibid. 10.VI.2012 leg. J. Bedek (CBSSC IT3849); ♀ ibid. leg. L. Deharveng, A. Beddos (CBSSC IT3850); 1 juv. ibid. leg. L. Kekelj (CBSSC IT3378); ♂ Croatia, Lika, Pazarište, Vranovine, Vranovinski ponor (CCC No. HR00490) 44,6361639727 °N, 15,2731928977 °E, 16.VII.1967 leg. Deeleman (SMNS 5276); 2 ♂♂ Croatia, Velebit, Pazarište, Japage, špilja Japa (CCC No. HR00344), 44,6312734108 °N, 15,1354392714 °E, 14.VIII.2006, leg. J. Bedek (CBSSC IT544); 3 ♂♂, 2 ♀♀ Croatia, Lika, Gospić, Mušaluk, Pećina pri mušalučkom donjem selu (a cave unknown at present), 12.IX.1964 leg. E. Pretner (ZZDBE 0899); ♂, ♀ Croatia, Lika, Gospić, Klanac, Grčka pećina (a cave unknown at present), 17.VII.1963 leg. Deeleman (SMNS 5344); ♂, 7 ♀♀ Croatia, Lika, Pazarište, Mlakva, Mlakvena greda (a cave unknown at present), 9.VII.1965 leg. Deeleman (SMNS 5295).

Other material (for DNA analyses): 2 ♂♂, 4 ♀♀, 1 juv. Croatia, Lika, Donji Kosinj, Lipovo polje, Markov ponor (CCC No. HR01480), 44,7653017089 °N, 15,1771778411 °E, 19.X.2011, leg. J. Bedek (CBSSC IT4113); ♂, 2 ♀♀ ibid. leg. M. Lukić (CBSSC IT2601); ♀ Croatia, Lika, Ličko Lešće, Pećina, 24.VI.2011 leg. M. Lukić (CBSSC IT3338); ♂, 3 ♀♀, 3 juv. Croatia, Lika, Perušić, Studenci, Milkovići, Budina špilja (CCC No. HR01195), 44,716915063 °N, 15,3613735717° E, 11.VI.2011, leg. N. Raguž (CBSSC IT3371); 1 juv. Croatia, Lika, Perušić, Sitvuki, Sitvukova pećina, 44,6786713198 °N, 15,3453423752 °E, 8.VIII.2014, leg. K. Cindrić (CBSSC IT3384); ♀ Croatia, Lika, Perušić, Grabovača, Medina pećina, 44,6389475032 °N, 15,3651981516 °E, 8.VIII.2014, leg. T. Dražina (CBSSC IT3380); ♀ Croatia, Lika, Perušić, Grabovača, Amidžina pećina, 44,6373404989 °N, 15,3639653667 °E, 11.V.2014 leg. K. Cindrić (CBSSC IT3379).

*Coordinates from Croatian Agency for the Environment and Nature (2017b).

Diagnosis. A medium-sized species characterized by a wide and terminally broadly rounded exopod of male pleopod 1, and outer margin deeply concave at about half of its length; male pereopod 7 merus with a caudal hook-shaped lobe on its proximal part, and pronounced hump on carpus dorsal margin; male pleopod 2 endopod with a short bifid terminal seta; antennal flagellum with up to 10 articles; antennula with up to seven aesthetascs.

Description. Maximum body length: ♂, 6.9 mm; ♀, 8.5 mm. Body (Fig. 2) depigmented, dorsal surface smooth. *Cephalon* (Fig. 3A) eyes absent, suprantennal line bent downwards, antennal lobes quadrangular with a central depression. *Pereon* with almost parallel sides, tergites smooth with scattered flask-shaped scale-sensilla (Fig. 3B). Posterior margin of pereonite 1 convex, of pereonites 2 and 3 straight, and of pereonites 4–7 progressively more concave. *Pleon* narrower than pereon, numerous gland pores laterally on pleonites 4 and 5. Pleonites 3–5 with small posterior points visible in dorsal view (Fig. 3C). *Telson* median distal part with concave sides and broadly rounded apex and lateral gland pores (Fig. 3C). *Antennula* (Fig. 3D) of three articles; first article longer than second and third; third article flattened and bearing up to seven aesthetascs on the apical margin. *Antenna* (Fig. 3E) with fifth article as long as flagellum; flagellum with up to 10 articles, with one row of aesthetascs on the second, third and sometimes fourth, fifth, sixth, seventh and eighth article. *Right mandible* with one penicil, lacinia mobilis toothed, pars molaris oval in shape with one penicil (Fig. 4A). *Left mandible* with three penicils, pars molaris oval in shape without penicils (Fig. 4B). *Maxillula* outer branch with 5+6 teeth, apically entire, and two slender stems; inner branch with three penicils, outer and middle ones subequal, inner one distinctly longer (Fig. 4C). *Maxilla* with setose and bilobate apex, inner lobe smaller (Fig. 4D). *Maxilliped* endite narrow, with a large and segmented apical penicil; palp distally with three rounded lobes and one setose setae on outer margin; basal article with two compound small setae; basis with a rounded outer lobe protruding posteriorly and a margin covered with long setae (Fig. 4E). *Pereopods* with an ungual seta and a large, bifid and setose dactylar seta (Fig. 5A). *Uropod* (Fig. 3C) with protopod and endopod slightly grooved on outer margin; endopod distinctly shorter than exopod, more proximally inserted. Numerous gland pores on protopod lateral margin.

Fig. 2. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. *in situ* in Croatia, Lika, Perušić, Grabovača, Medina pećina (photo J. Bedek).

Male: *Pereopod 1–4* (Fig. 5A) similar in shape, with carpus and merus bearing numerous short scales on rostral surface. *Pereopod 7* (Fig. 5B–C) ischium with straight sternal margin; merus with concave sternal margin and a setose caudal hook-shaped lobe in the proximal part bearing one seta; carpus dorsal margin with a pronounced hump in it's medial part. *Genital papilla* (Fig. 6A) simple, with a

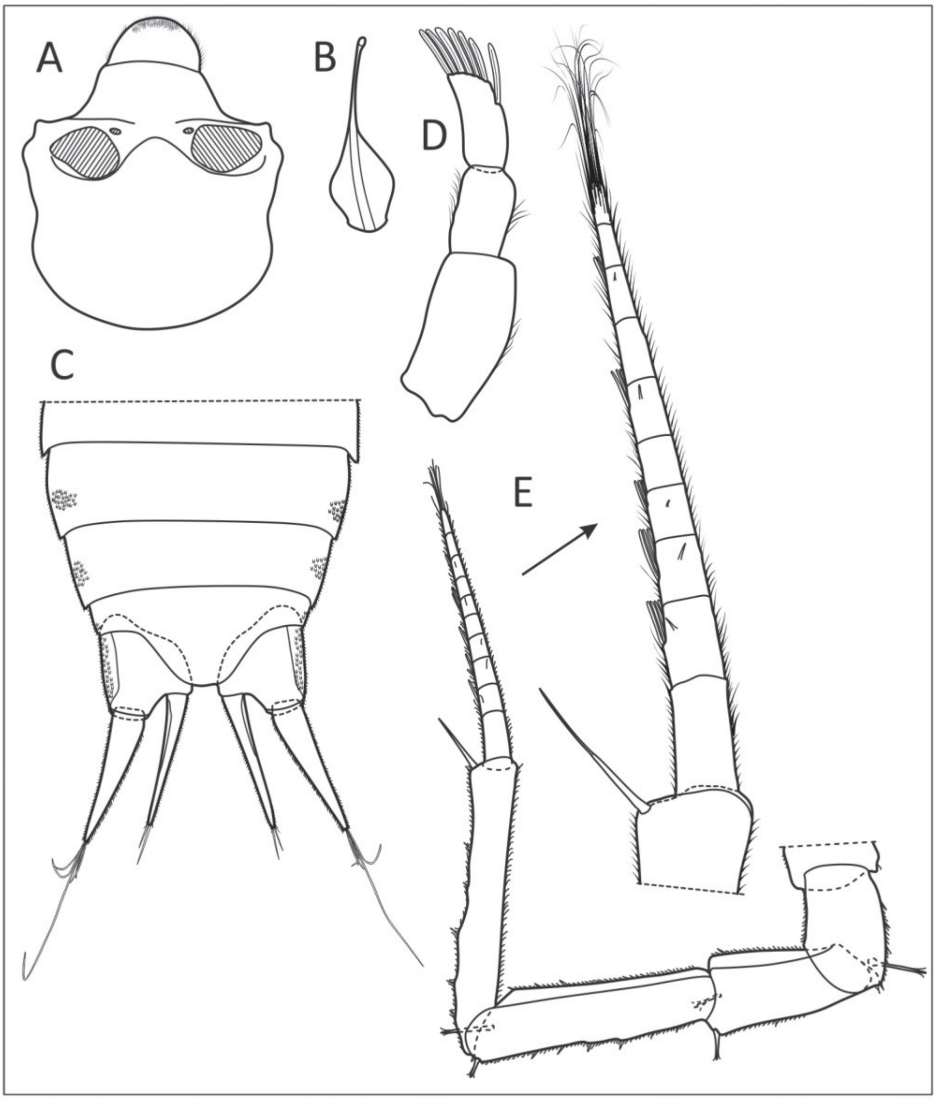

Fig. 3. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. paratype ♀: A, cephalon; paratype ♂: B, dorsal scale-sensilla; C, pleonites 4, 5, telson and uropods; D, antennula; E, antenna.

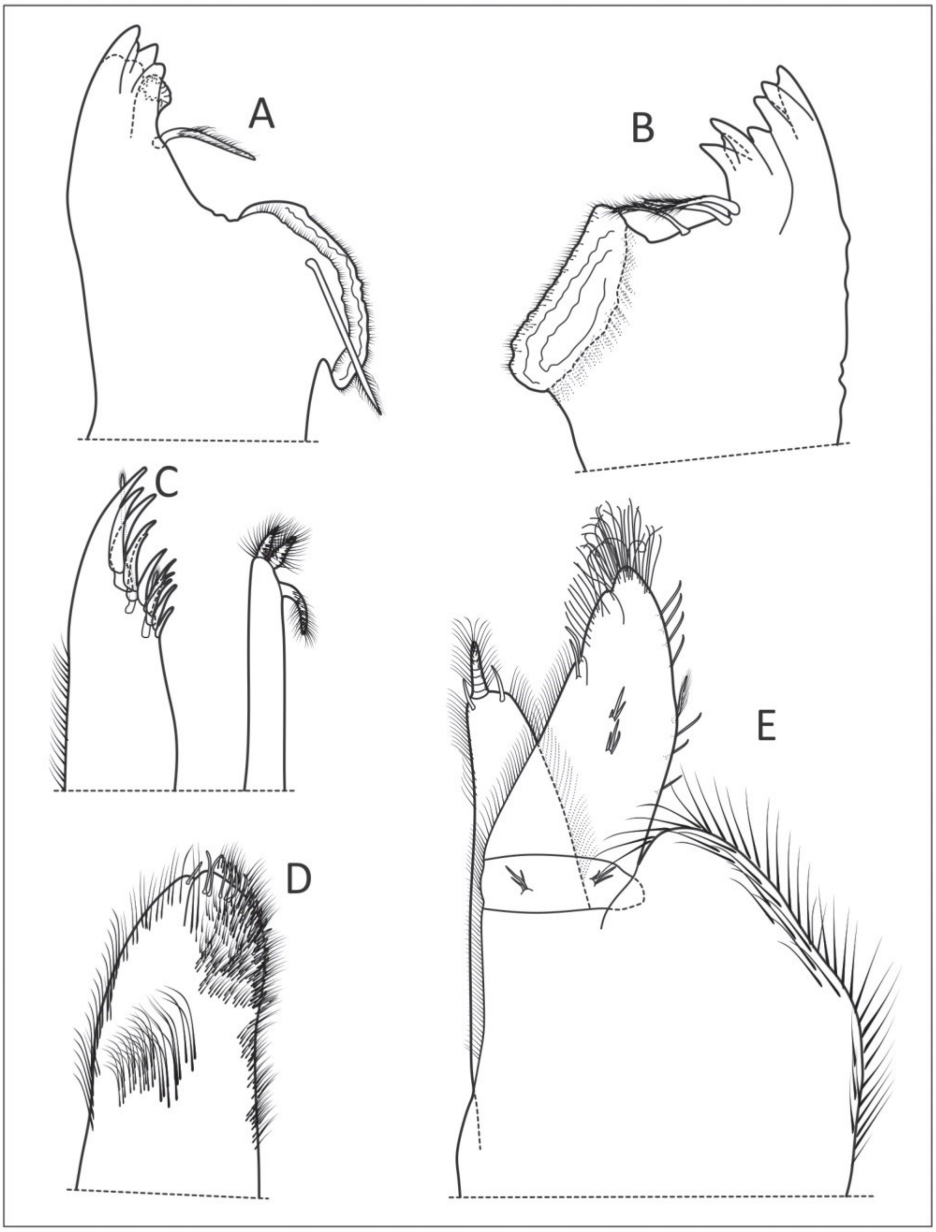

Fig. 4. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. paratype ♂: A, right mandible; B, left mandible; C, maxillula; D, maxilla; E, maxilliped.

Fig. 5. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. paratype ♂: A, pereiopod 1; B, pereiopod 7 rostral view with enlargement of merus and carpus; C, pereiopod 7 merus caudal view.

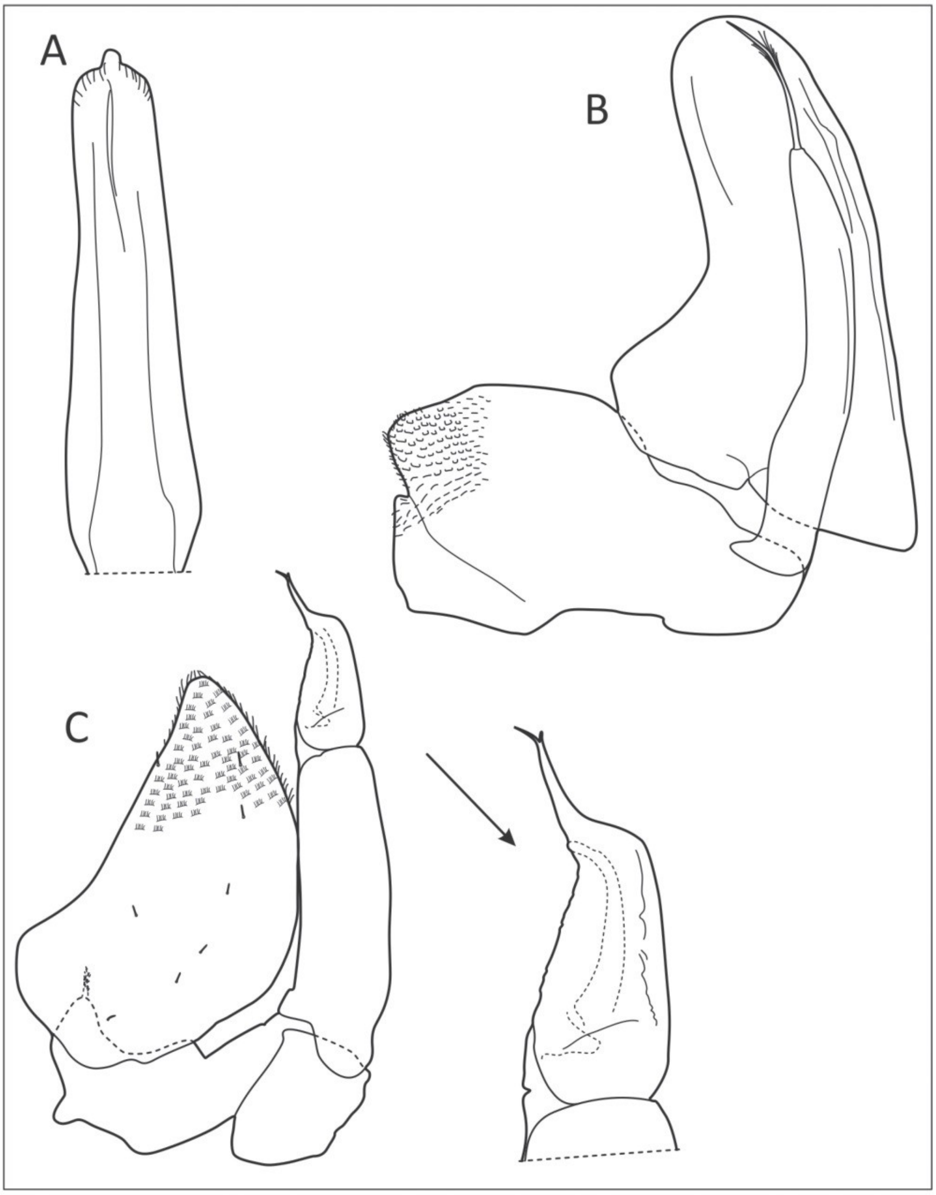

Fig. 6. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. paratype ♂: A, genital papilla; B, pleopod 1; C, pleopod 2 with enlargement of endopod third article.

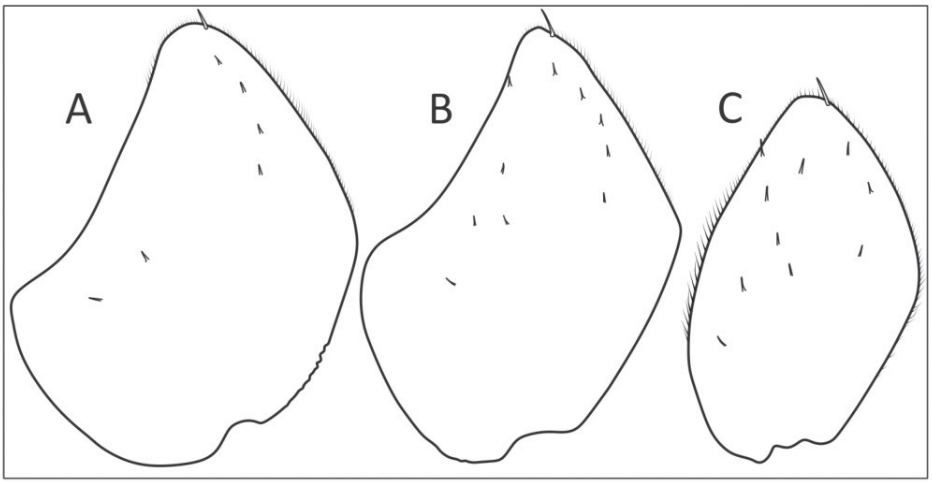

Fig. 7. *Alpioniscus* (*Illyrionethes*) *iapodicus* n. sp. paratype ♂: A, pleopod 3 exopod; B, pleopod 4 exopod; C, pleopod 5 exopod.

rounded apical part. *Pleopod 1* (Fig. 6B) exopod wide, terminally broadly rounded, somewhat less than 3 times as long as wide in its medial part, deeply concave outer margin; endopod narrow with almost parallel sides, armed with a long apical seta. *Pleopod 2* (Fig. 6C) exopod triangular with convex outer margin; endopod of three articles, slightly longer than exopod, third article about three times shorter than second with a strong bifid terminal point. *Pleopod 3-5* exopods as in Fig. 7A-C.

Etymology. The new species is named after the Iapydes (Lat. Iapodes; Hr. Japodi), an ancient tribe inhabiting the montane areas of the Northern Dinaric karst, including the Lika, Kordun and Pounje regions.

Remarks.

Alpioniscus iapodicus n. sp. belongs to the *strasseri* group, which comprises *A. strasseri* (Verhoeff, 1927), *A. balthasari* (Frankenberger, 1937), *A. christiani* Potočnik, 1983 and *A. absoloni* (Strouhal, 1939) (sensu Bedek & Taiti, 2011). It shows closest affinities with *A. balthasari*, widely distributed in Dalmatia, up to the eastern part of Mt Velebit to the northwest and Tomislavgrad in Hercegovina to the east (Bedek, *et al*., 2011). Upwards to the north it is replaced by *A. iapodicus* n. sp., clearly differing from the other species of the *strasseri*-group by the: I) position of the hook-shaped lobe of the male merus 7: on the inner side (*A. iapodicus*) *vs*. ventrally positioned (all other *strasseri* group representatives), II) carpus 7 dorsal hump placed in its medial part (*A. iapodicus*) *vs*. proximally positioned (all other *strasseri* group representatives), and III) pleopod 1 exopod proximally wide (*A. iapodicus*) *vs*. narrow (all other *strasseri* group representatives) (Arcangeli, 1932; Buturović, 1955; 1957; Frankenberger, 1937; Kesselyák, 1930; Horvatović, 2014; Potočnik, 1983; Strouhal, 1938; 1939a; 1939b; Verhoeff, 1927).

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Paper 2

Bedek J, Taiti S, Bilandžija H, Ristori E, Baratti M (2019) Molecular and taxonomic analyses in troglobiotic *Alpioniscus* (*Illyrionethes*) species from the Dinaric Karst (Isopoda: Trichoniscidae). Zoological Journal of the Linnean Society 187: 539–584. https://doi.org/10.1093/zoolinnean/zlz056

Online article available at https://academic.oup.com/zoolinnean/article/187/3/539/5555552?guestAccessKey=0f6df46c-68d7-4aad-b159-33382345fd55

Paper 3

Bedek J, Gottstein S, Taiti S (2019) Taxonomy of *Alpioniscus* (*Illyrionethes*): *A. magnus* and three new species from the Dinaric Karst (Isopoda: Oniscidea: Trichoniscidae). Zootaxa 4657: 483–502. https://doi.org/10.11646/zootaxa.4657.3.4

Online article available at https://www.biotaxa.org/Zootaxa/article/view/zootaxa.4657.3.4

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Taxonomy of *Alpioniscus* (*Illyrionethes*): *A. magnus* and three new species from the Dinaric Karst (Isopoda: Oniscidea: Trichoniscidae)

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Abstract

Alpioniscus (*Illyrionethes*) is a widespread subgenus of Trichoniscidae in the Dinaric Karst with 15 nominal troglobiotic species. Here we redescribe *Alpioniscus (Illyrionethes) magnus* and describe three new species (*A. lossinii* **n. sp.**, *A. drazinai* **n. sp.**, and *A. mandalinae* **n. sp.**) restricted to coastal areas. As a result, 18 nominal *Illyrionethes* species are known from the Dinaric Karst.

Key words: Adriatic coast, cave fauna, new species, terrestrial isopods, troglobionts, Trichoniscinae

Introduction

The subgenus *Illyrionethes* Verhoeff, 1927 of the genus *Alpioniscus* Racovitza, 1908 is widespread in caves of the Dinaric Karst, from Trieste in Italy to Durmitor in Montenegro (Schmalfuss 2003; Horvatović 2014). The recent integrative taxonomic study of *Illyrionethes* species in the Dinaric Karst revealed 19 troglobiotic species, four of which still undescribed (Bedek *et al.* 2017; Bedek *et al.* 2019). They grouped into three different lineages (*strasseri*-, *heroldi*- and *magnus*-lineage), with overlapping ranges. In this paper, we analyse the species of the *magnus*-lineage: we redescribe *Alpioniscus* (*Illyrionethes*) *magnus* (Frankenberger, 1938) from the island of Brač and describe three new species from the islands of Mali Lošinj and Dugi otok, and from the coastal area near Šibenik.

Material and methods

Specimens were hand collected with tweezers, fixed and stored in 75% ethanol with glycerol or 96% ethanol. Several specimens were dissected and mounted for micropreparations in Hoyer's medium (Anderson 1954). For identifications, the following appendages were usually dissected: antennae, antennulae, male pereopods 1 and 7, genital papilla and male pleopods 1 and 2. Specimens were examined under a Zeiss Stemi 2000-C, Zeiss Primo Star and Nikon Labophot microscopes. Micropreparations were photographed using Canon EOS 40D and EOS Utility software. Drawings were made either from photographs or with the aid of a camera lucida. Body size, male pereopod 7 carpus hump (ending point position, top position) and carpus length were measured (for terminology see Bedek *et al.* 2019). The ratios are expressed in arithmetic mean ± SD. The examined material, description, etymology and remarks are given. The following numerical characters were counted: number of (1) antennular aesthetascs, (2) antennal flagellum articles, (3) antennal flagellum articles bearing aesthetascs, and (4) setae on the male pereopod 1 carpus. The terminology used in species description is mainly based on Vandel (1960, 1962). The locality coordinates used the WGS84 map datum.

Abbreviations: CBSSC—Croatian Biospeleological Society Collection, Zagreb, Croatia; CCC—Croatian Cave Cadaster, hosted by Ministry of Environment and Energy, Zagreb, Croatia (Croatian Agency for the Envi-

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ronment and Nature 2015); MZUF—Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia La Specola, Florence, Italy.

Taxonomy

Family Trichoniscidae Sars, 1899

Subfamily Trichoniscinae Sars, 1899

Genus *Alpioniscus* Racovitza, 1908

Subgenus *Illyrionethes* Verhoeff, 1927

Alpioniscus* (*Illyrionethes*) *magnus (Frankenberger, 1938)

(Figs 1–4, 15)

Titanethes albus.—Wettstein 1914: 59–64.
Illyrionethes magnus Frankenberger 1938: 27, 30–33, figs 3–7.—Strouhal 1939a: 7, 23.—1939b: 115, 127–128, fig. 1.—1939c: 17–18.—1939d: 17–18.—1940: 94; Frankenberger & Strouhal 1940: 449.
Alpioniscus (*Illyrionethes*) *magnus*.—Vandel 1946: 155.—Buturović 1957: 7–49, fig. 24.—Schmölzer 1965: 58, figs 218–219.—Karaman 1966: 378.—Potočnik 1993: 85, 178.—Tabacaru 1996: 35.—Horvatović 2014: 173, 175, 223. —Bedek *et al.* 2019: figs 3, 5.
Alpioniscus magnus.—Vandel 1947: 271.—Potočnik 1989: 64.—Schmalfuss 2003: 14.—Bedek *et al.* 2006: 14, 92.—Jalžić *et al.* 2010: 20.—Bedek *et al.* 2011: 240, 273–275, fig. 15—Jalžić *et al.* 2013: 13, 30, 40, 2 figs (not numbered).
Alpioniscus.—Giachino *et al.* 2011: 360 [partim: Jama kod Matešića stana].

Material examined. Croatia, Dalmatia, Brač Island: *Nerežišće, Podgažul, Bazgovača (cave CCC HR01146)*, 43.3065°N, 16.6222°E, 1 female, 1 juv., 29 September 1996, leg. M. Franičević (CBSSC IT1665); 5 males, 1 male juv., 3 females, 1 female juv., 4 August 2004, leg. R. Ozimec and B. Jalžić (CBSSC IT1664; IT1667); 1 male juv., 26 October 2006, leg. R. Ozimec (CBSSC IT1669); 2 males juv., 1 female, 1 juv., 22 October 2007, leg. J. Bedek (CBSSC IT1666; IT1672); 2 females, 5 January 2009, leg. F. Kljaković Gašpić and M. Pavlek (CBSSC IT1670; IT1671); 8 males, 9 females, 5 October 2009, leg. M. Lukić and M. Novokmet (CBSSC IT2094; IT2095; IT2097); 3 males, 2 females, 3 females juv., 30 June 2017, leg. M. Pavlek and T. Rožman (CBSSC IT4321; IT4322).

Nerežišće, Neorić, Činjadra (cave CCC HR01149), 43.3398°N, 16.5994°E, 5 males, 1 female, 1 female juv., 5 August 2004, leg. R. Ozimec and B. Jalžić (CBSSC IT4323; IT4325); 6 males, 2 males juv., 6 females, 22 October 2007, leg. M. Lukić and J. Bedek (CBSSC IT1356; IT1357); 1 female juv., 3 juvs, 5 January 2009, leg. H. Bilandžija and B. Jalžić (CBSSC IT1368; IT4326; IT4327); 6 males, 3 males juv., 12 females, 3 females juv., 1 July 2017, leg. M. Pavlek and T. Rožman (CBSSC IT4328; IT4329).

Nerežišće, Zvirine stope, Dobra jama (cave CCC HR01151), 43.3085°N, 16.5808°E, 6 males, 8 females, 3 females juv., 2 juv., 5 August 2004, leg. R. Ozimec, P. Rade and B. Jalžić (CBSSC IT4365; IT4366; IT4367); 1 male, 1 female, 22 October 2007, leg. H. Bilandžija (CBSSC IT4368).

Gornji Humac, Grimač, Jama kod Matešića stana (cave), 43.3059°N, 16.7511°E, 1 male, 1 male juv., 5 females, 1 female juv., 4 juvs, 6 August 2004, leg. R. Ozimec and B. Jalžić (CBSSC IT4351; IT4352); 3 males, 1 male juv., 3 females, 2 females juv., 1 juv., 25 October 2006, leg. H. Bilandžija (CBSSC IT4353); 2 females, 2 juvs, 13 March 2011, leg. D. Hmura, A Čukušić and P. Kutleša (CBSSC IT4354; IT4355; IT4356); 2 males, 1 male juv., 4 males juv., 1 female juv., 2 juvs, 14 March 2011, leg J. Bedek, M. Pavlek and A. Komerički (CBSSC IT2394; IT4357; IT4358; IT4359).

Sumartin, Podstražišće, Jama kod Podstražišća (cave), 3 males, 3 females, 3 August 2004, leg. R. Ozimec (CBSSC IT4375).

Pučišća, Jasenovo brdo, Jama na Jasenovom brdu (cave CCC HR00554), 43.3368°N, 16.7440°E, 2 males, 31 July 2003, leg. M. Dropulić (CBSSC IT4376).

Povlja, Jama u Kupinovac (cave), 1 male, 1 female, 24 February 2002, leg. M. Franičević (CBSSC IT4377).

Selca, Kale, Trgud, Jama u Lukeša docu (cave), 43.2858°N, 16.8411°E, 3 males, 1 male juv., 4 females, 1 female juv., 3 juvs, 20 July 2007, leg. R. Ozimec and B. Jalžić (CBSSC IT2603; IT2606).

Pučišća, Jama za Mahrincem (cave CCC HR00293), 43.3445°N, 16.7409°E, 2 males, 1 male juv., 6 females, 2 females juv., 5 August 2004, leg. B. Jalžić and R. Ozimec (CBSSC IT4330; IT4331); 4 males, 1 male juv., 7 females, 24 October 2007, leg. J. Bedek, H. Bilandžija and M. Lukić (CBSSC IT2281; IT2282; IT4332); 1 male, 1 male juv., 8 females, 2 juvs, 5. January 2009, leg. M. Pavlek and F. Kljaković Gašpić (CBSSC IT4333; IT4334); 3 males, 4 males juv., 4 females, 1 female juv., 4 juvs, 12 March 2011, leg. A. Čukušić, N. Ragož and L. Đud (CBSSC IT4335; IT4336; IT4339).

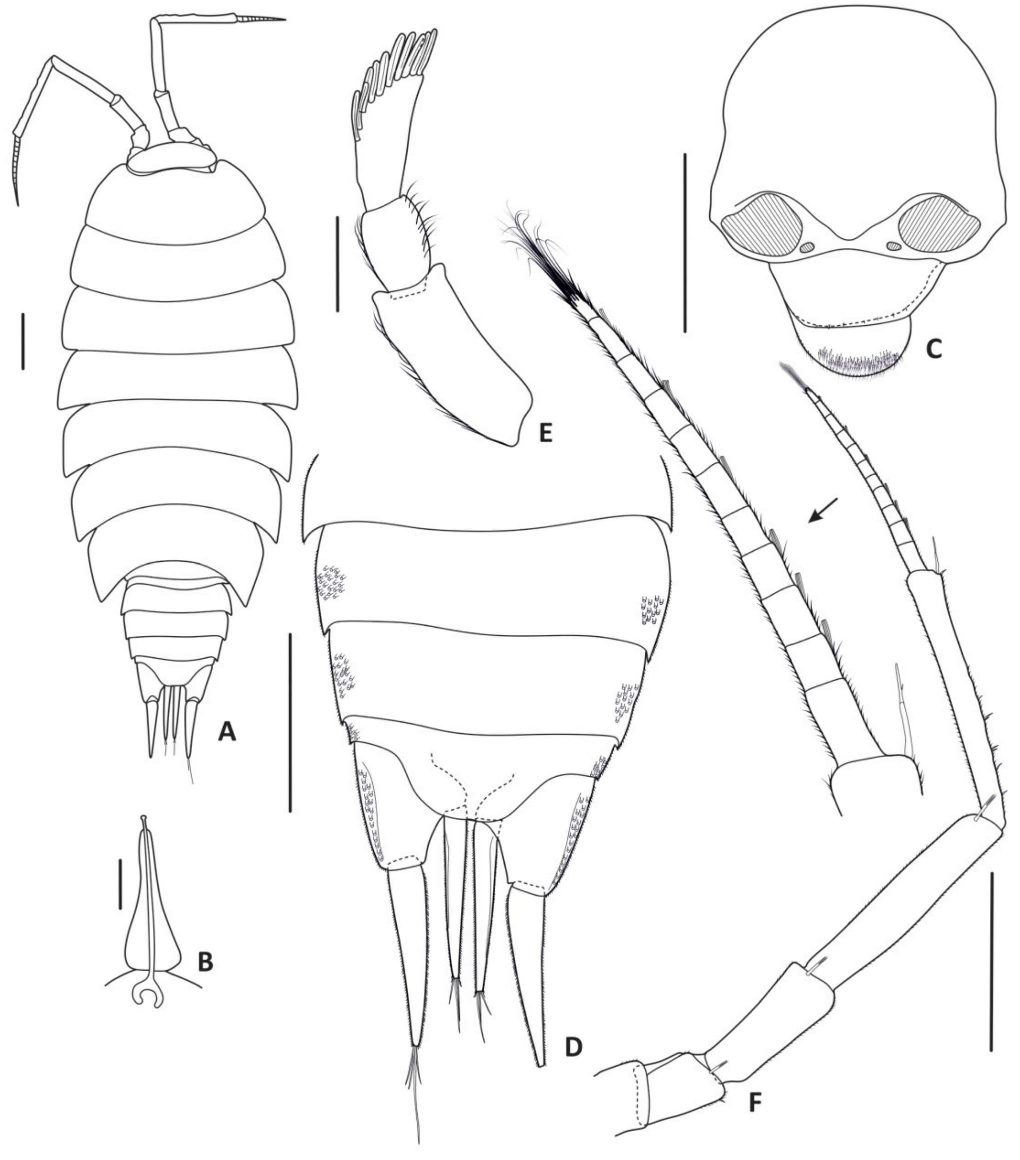

FIGURE 1. *Alpioniscus* (*Illyrionethes*) *magnus* (Frankenberger, 1938). A, topotype female CBSSC IT1664 from Bazgovača. B–F, topotype male CBSSC IT1664 from Bazgovača. A, habitus, dorsal view; B, dorsal scale-seta; C, cephalon, dorsal view; D, pleonites 4, 5, telson and uropods; E, antennula; F, antenna with enlargment of flagellum. Scale bars: A, C, D, F = 1 mm; B = 0.01 mm; E = 0.1 mm.

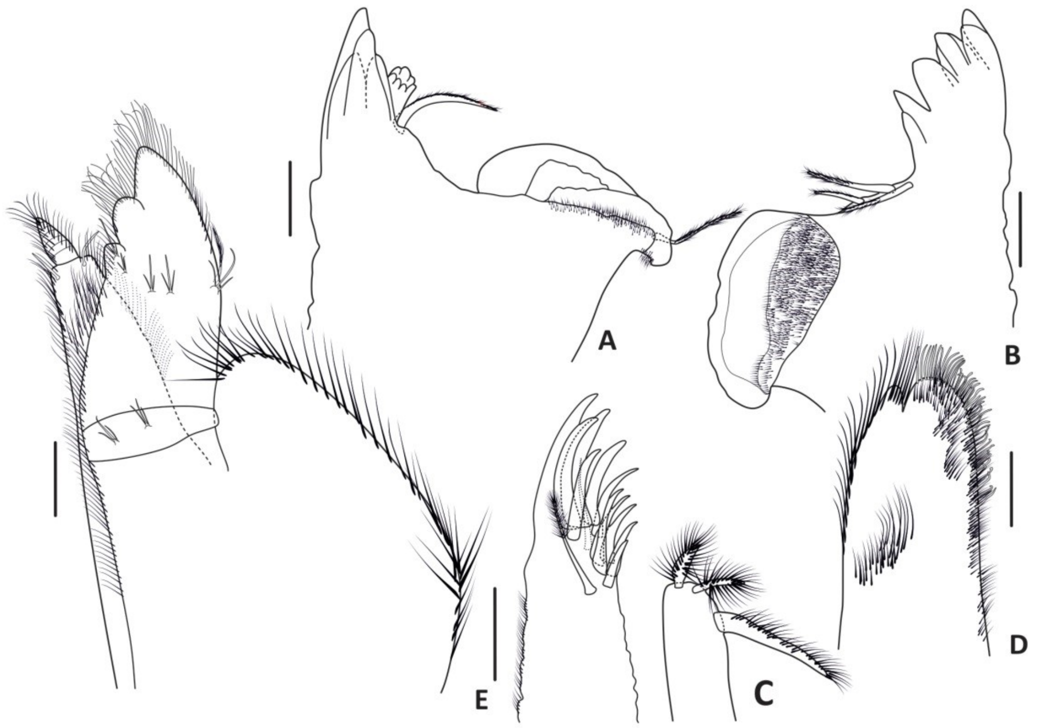

FIGURE 2. *Alpioniscus* (*Illyrionethes*) *magnus* (Frankenberger, 1938). Topotype male CBSSC IT1664 from Bazgovača. A, right mandible; B, left mandible; C, maxillula; D, maxilla; E, maxilliped. Scale bars: 0.1 mm.

Selca, Ješkalovica, Ješkalovica (cave CCC HR01130), 43.2999°N, 16.8393°E, 2 males, 3 females, 3 juvs, 4 January 2009, leg. M. Pavlek and F. Kljaković Gašpić (CBSSC IT2608; IT2610); 1 male, 1 male juv., 1 juv., 21 February 2010, leg. P. Bregović (CBSSC IT2611); 1 male juv., 3 females, 2 females juv., 5 juvs, 28 February 2010, leg. N. Raguž and P. Bregović (CBSSC IT2612; IT2613); 4 females juv., 7 juvs, 12 March 2011, leg. P. Bregović, D. Hmura and P. Kutleša (CBSSC IT2615; IT2617; IT2618).

Postira, Dol, Dunaj, Kaptaža K-2 (water capping tunnels-cave), 43.3592°N, 16.6230°E, 2 males, 2 males juv., 1 female juv., 28 February 2010, leg. B. Jalžić, H. Bilandžija (CBSSC IT4361); 1 male, 3 males juv., 4 females, 6 females juv., 8 juvs, 12 March 2011, leg. A. Komerički and J. Bedek (CBSSC IT4362; IT4363; IT4364).

Postira, Škrip, Minjera (mine-cave CCC HR02009), 43.3613°N, 16.6063°E, 5 males, 2 females, 1 juv., 24 October 2007, leg. H. Bilandžija, J. Bedek and B. Jalžić (CBSSC IT2283; IT2284; IT4342); 1 male, 3 males juv., 4 females, 1 female juv., 26 juvs, 13 March 2011, leg. J. Bedek, A. Komerički, N. Raguž, M. Pavlek and L. Đud (CBSSC IT2392; IT2393; IT4343; IT4344; IT4345; IT4347; IT4349); 1 male, 1 female juv., 23 March 2018, leg. B. Jalžić (CBSSC IT4350).

Nerežišće, Drašnice, Spuža (cave), 43.3065°N, 16.6222°E, 1 male, 4 females juv., 3 juvs, 23 March 2018, leg. B. Jalžić (CBSSC IT4372).

Supetar, Tanki ratac (cave), 43.360229°N, 16.569356°E, 1 female, 1 juv., 29 June 2017, leg. T. Rožman (CBSSC IT4340).

Selca, Osridke, Žejava (cave CCC HR01147), 43.2846°N, 16.8040°E, 2 males, 1 female, 6 females juv., 10 juvs, 23 October 2007, leg. H. Bilandžija (CBSSC IT4369; IT4370).

Type locality. Croatia, Dalmatia, Brač Island: Nerežišće, Podgažul, Bazgovača (cave CCC HR01146); Supetar, Donji Humac, Kopačina (cave); Supetar, Tanki ratac (cave); Nerežišće, Neorić, Činjadra (cave CCC HR01149); Nerežišće, Filipovića jama (cave); Pučišća, Jama za Mahrincem (cave CCC HR00293); Pučišća, Spilja pod Vrhom (unknown cave) (Frankenberger 1938).

Redescription. Maximum length: male, 10.2 mm; female, 11.2 mm. Colourless *body*, *pereon* with almost parallel sides, *pleon* narrower than pereon (Fig. 1A). Dorsum smooth, with some triangular scale-setae (Fig. 1B). Some gland pores on lateral margins of pleonites 4, 5, telson and uropodal protopods (Fig. 1D).

FIGURE 3. *Alpioniscus* (*Illyrionethes*) *magnus* (Frankenberger, 1938). Topotype male CBSSC IT1664 from Bazgovača. A, pereopod 1 with enlargment of dactylus; B, pereopod 7 rostral view with enlargement of merus and carpus; C, pereopod 7 merus caudal view with enlargment of hook. Scale bars: A, B = 1 mm; C = 0.1 mm.

Cephalon (Fig. 1C) with suprantennal line bent downwards in middle; antennal lobes quadrangular. *Eyes* absent. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and of pereonites 4–7 progressively more concave. *Pleonites 3–5* with small posterior points visible in dorsal view. Distal part of *telson* with concave sides and broadly rounded apex (Fig. 1D).

Antennula (Fig. 1E) of three articles, distal article flattened and bearing five to 11 aesthetascs on apical margin. *Antenna* (Fig. 1F) smooth; flagellum of eight to 12 articles with one row of aesthetascs on four to six different articles, always on second and third.

Mandibles (Fig. 2A, B) with one penicil in right and three penicils in left; molar process with one penicil in right.

Maxillula (Fig. 2C) outer branch with 5+6 teeth, apically entire, and two slender stalks; inner branch with three penicils, outer and middle subequal, inner distinctly longer. *Maxilla* (Fig. 2D) with setose and bilobate apex, inner lobe distinctly wider than outer one.

Maxilliped (Fig. 2E) endite narrow, with large segmented apical penicil; palp distally with three rounded lobes, basal article with two small compound setae; basis with rounded outer lobe protruding posteriorly and covered with long setae on margin.

Pereopods similar in shape, ungual seta simple, dactylar seta bifid and setose (Fig. 3A).

Uropod (Fig. 1D) with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

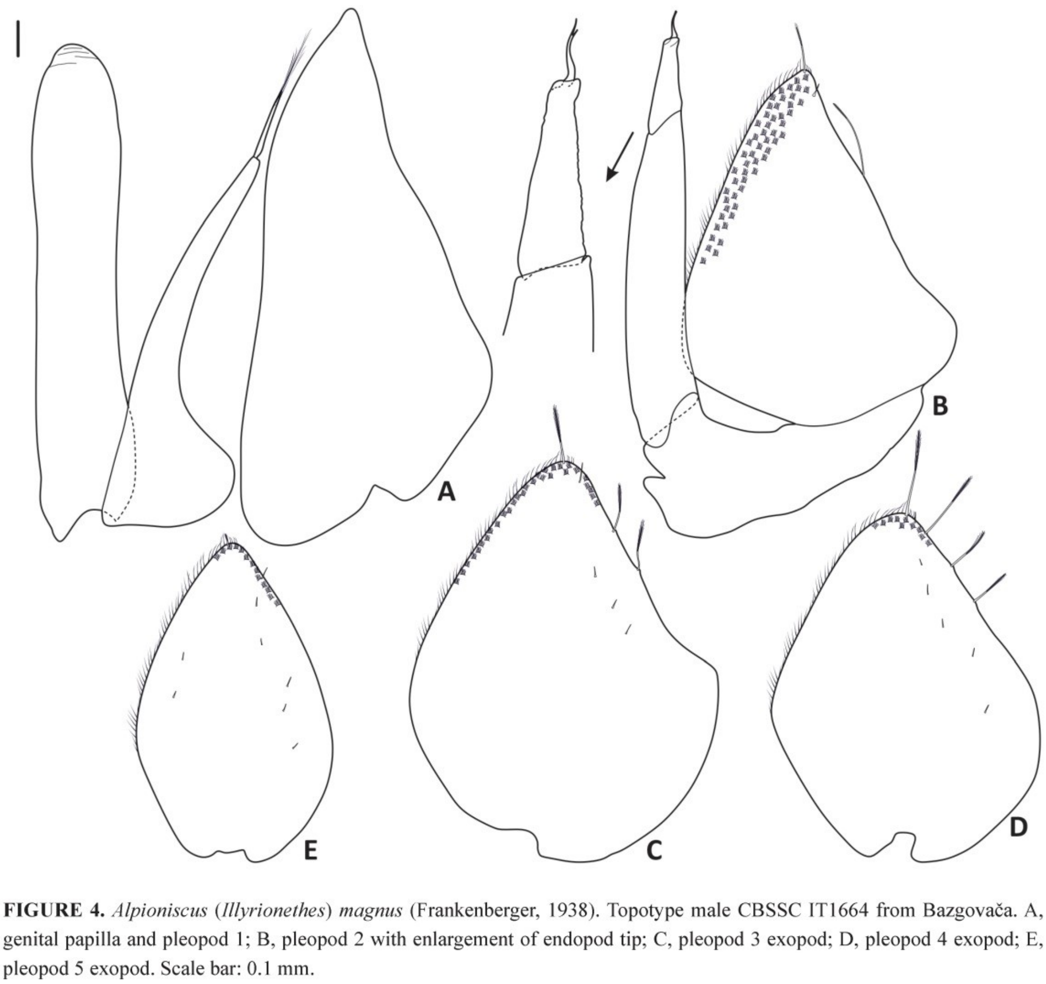

FIGURE 4. *Alpioniscus* (*Illyrionethes*) *magnus* (Frankenberger, 1938). Topotype male CBSSC IT1664 from Bazgovača. A, genital papilla and pleopod 1; B, pleopod 2 with enlargement of endopod tip; C, pleopod 3 exopod; D, pleopod 4 exopod; E, pleopod 5 exopod. Scale bar: 0.1 mm.

Male: *Pereopod 1* (Fig. 3A) carpus bearing six to seven setae. *Pereopod 1 and 2* with propodus and carpus bearing numerous short scales on rostral surface. Merus of *pereopods 1–3* with sternal margin straight, of *pereopods 4–6* slightly concave with small lobe proximally. *Pereopod 7* (Fig. 3B, C) ischium with straight sternal margin; merus with slightly concave sternal margin and hook-shaped lobe proximally, with scales and one seta at apex; carpus with dorsal hump on tergal margin, carpus length: top hump position 1.69±0.11 (N=10), carpus length: ending hump position 1.24±0.04 (N=10).

Genital papilla (Fig. 4A) with rounded apical part.

Pleopod 1 (Fig. 4A) exopod triangular with acute apex, inner and outer margins slightly sinuous; endopod narrow with wide basal part and concave outer margin, with apical seta distinctly shorter than basal article.

Pleopod 2 (Fig. 4B) exopod triangular with setae on outer margin; endopod of two articles, slightly longer than exopod, distal article progressively narrower towards apex with strong bifid terminal seta.

Pleopod 3–5 exopods as in Fig. 4C–E.

Remarks. *Alpioniscus magnus* is one of the largest species of Dinaric *Illyrionethes*. It is characterized by the presence of a hump on the male pereopod 7 carpus, together with *strasseri*-lineage species (*A.* (*I.*). *strasseri* (Verhoeff, 1927), *A.* (*I.*). *balthasari* (Frankenberger, 1937), *A.* (*I.*). *christiani* Potočnik, 1983, *A.* (*I.*). *iapodicus* Bedek, Horvatović and Karaman, 2017, *A. hirci* Bedek & Taiti, 2019, *A. velebiticus* Bedek & Taiti, 2019), and *A.* (*I.*) *absoloni* (Strouhal, 1939a)). It differs from all these species in having a low and long tergal hump on the male pereopod 7 carpus, the male pleopod 1 exopod with acute, instead of rounded apex and slightly sinuous outer margin. This species is amphibious.

Alpioniscus (*Illyrionethes*) *lossinii* n. sp.

(Figs 5–8, 15)

http://zoobank.org/47E3E7D2-262F-4D2C-B50E-3C3322043DC2

Alpioniscus strasseri.—Bedek *et al.* 2011: 278 (partim: Medvjeđa špilja).
Alpioniscus (*Illyrionethes*) sp. 2.—Bedek *et al.* 2019: figs 3, 5.

Material examined. Croatia, Croatian Littoral, Mali Lošinj Island: ***Holotype*** male Ćunski, Rt. Lokvica, Medvjeđa špilja (cave), 44.6055°N, 14.4079°E, 25–28 March 2010, leg. J. Bedek (CBSSC IT4224).

Paratypes. 4 males, 1 male juv., 13 females, 3 juvs, same data as holotype (CBSSC IT2397); 1 male, 8 females, same locality, 20 March 2005, leg. J. Bedek (CBSSC IT2398); 2 males, 2 females, same locality and date, leg. M. Lukić (MZUF 9846); 3 males, 5 females, same locality, 6 March 2010, leg. B. Jalžić (CBSSC IT2400); 1 male, same locality, 2 March 2010, leg. J. Bedek (CBSSC IT2402).

Description. Maximum length: male, 4.9 mm; female, 5.3 mm. Colourless *body*, *pereon* with almost parallel sides, *pleon* narrower than pereon (Fig. 5A,B). Dorsum granulated, with ridges near posterior margins of cephalon, pereonites and pleonites 1–2, and some triangular scale-setae (Fig. 5C). Some gland pores on lateral margins of pleonites 4, 5 and telson (Fig. 5E).

Cephalon (Fig. 5D) with suprantennal line bent downwards in middle; antennal lobes rounded. Eyes absent. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and of pereonites 4–7 progressively more concave (Fig. 5A). Pleonites 3–5 with small posterior points visible in dorsal view (Fig. 5E). Distal part of telson with concave sides and broadly rounded apex (Fig. 5E).

Antennula (Fig. 5F) of three articles, distal article bearing five to seven aesthetascs. *Antenna* (Fig. 5G) with peduncle granulated; flagellum of eight to 10 articles with one row of aesthetascs on four to five different articles, always on a second and third article. *Buccal pieces* (Fig. 6) as in A. *magnus*.

Pereopods similar in shape, ungual seta simple, dactylar seta bifid and setose (Fig. 7A).

Uropod (Fig. 5E) with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male: *Pereopod 1* (Fig. 7A) carpus bearing five to six setae. *Pereopod 1 and 2* with propodus and carpus bearing numerous short scales on rostral surface. *Pereopods 5 and 6* with small lobe proximally on sternal margin. *Pereopod 7* (Fig. 7B,C) ischium with straight sternal margin; merus with slightly concave sternal margin and proximally with small hook-shaped lobe bearing up to five triangular scales and one large seta; carpus with straight sternal and tergal margins.

Genital papilla (Fig. 8A) with rounded apical part.

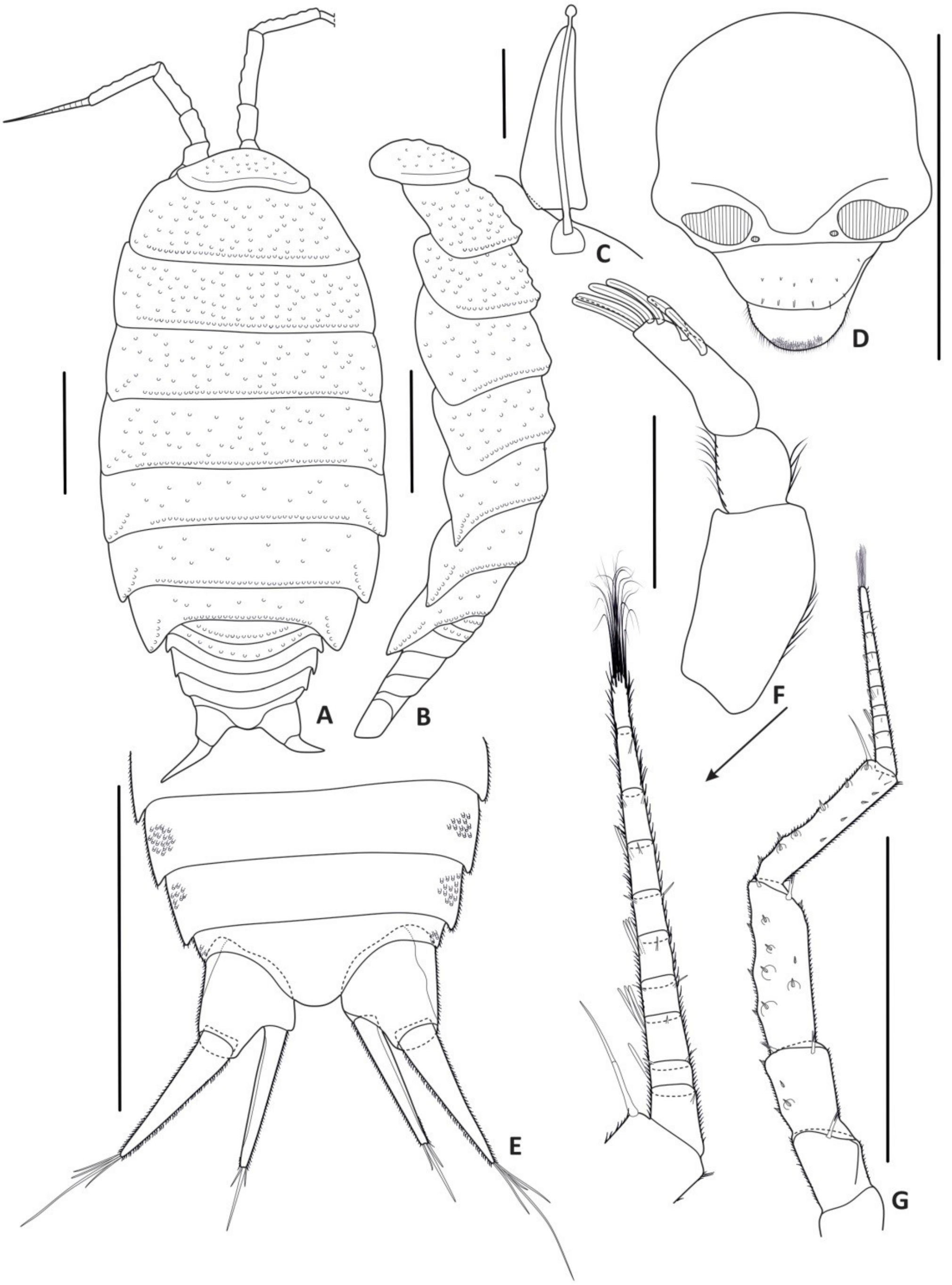

FIGURE 5. *Alpioniscus* (*Illyrionethes*) *lossinii* **n. sp.** A, B, paratype female CBSSC IT2379 from Medvjeđa špilja. C–G, paratype male CBSSC IT2379 from Medvjeđa špilja. A, habitus in dorsal view; B, pereonites and pleonites in lateral view; C, dorsal scale-seta; D, cephalon, dorsal; E, pleonites 4, 5, telson and uropods; F, antennula; G, antenna with enlargment of flagellum. Scale bars: A, B, D, E, G = 1 mm; C = 0.01 mm; F = 0.1 mm.

Pleopod 1 (Fig. 8A) exopod with distal part narrow and rounded apex, concave outer margin, slightly convex inner margin; endopod narrow, triangular, armed with long apical plumose seta.

Pleopod 2 (Fig. 8B) exopod subtriangular with slightly concave outer margin; endopod of two articles, slightly longer than exopod, distal article with posterior part narrower with strong and subapically bifid terminal seta.

Pleopod 3–5 exopods as in Fig. 8C–E.

Etymology. The species is named after the island of Lošinj (Lat. Lossinium).

Remarks. The new species is characterized by the lack of a hump on the tergal margin of the male pereopod 7 carpus, together with *A.* (*I.*). *haasi* (Verhoeff, 1931b), *A.* (*I.*) *heroldi* (Verhoeff, 1931a), *A.* (*I.*) *herzegowinensis* (Verhoeff, 1931a), *A.* (*I.*) *kratochvili* (Frankenberger, 1938), *A.* (*I.*) *tuberculatus* (Frankenberger, 1939), *A.* (*I.*) *verhoeffi* (Strouhal, 1938) and the two new species described below, *A.* (*I.*) *drazinai* and *A.* (*I.*) *mandalinae*. It differs from all these species by the narrow distal part of the male pleopod 1 exopod; from *A.* (*I.*) *heroldi* and *A.* (*I.*) *herzegowinensis* also in the shape of the hook on the male pereopod 7 merus.

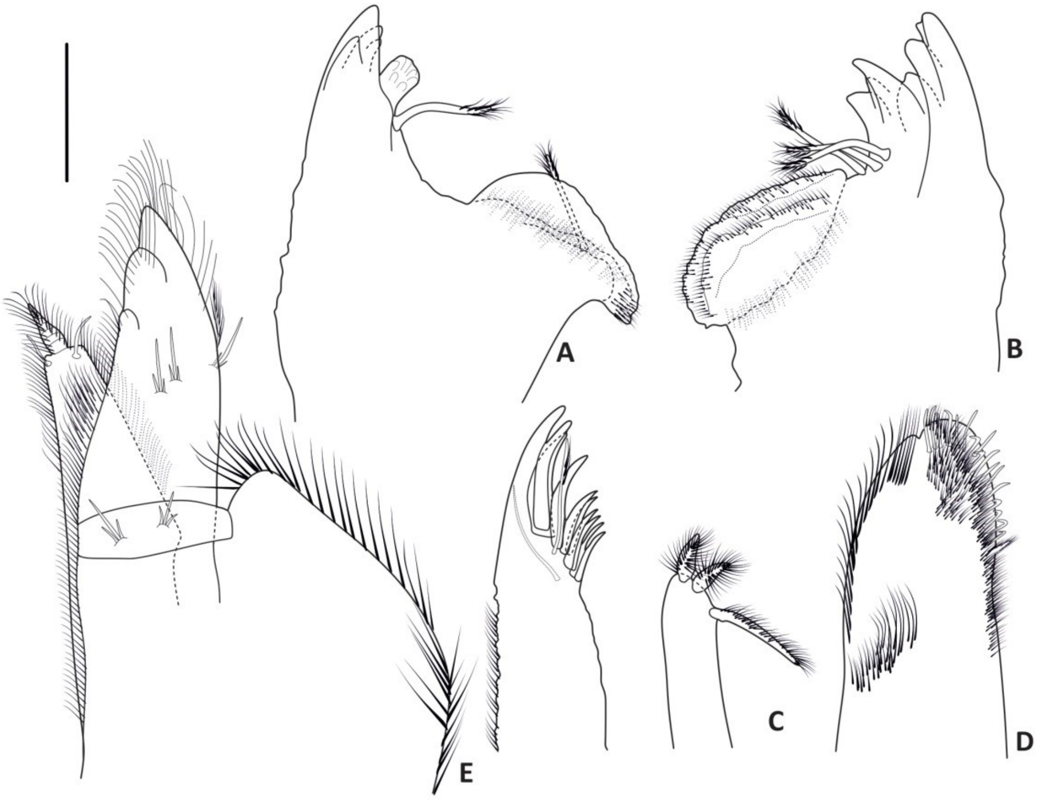

FIGURE 6. *Alpioniscus* (*Illyrionethes*) *lossinii* **n. sp.** Paratype male CBSSC IT2379 from Medvjeđa špilja. A, right mandible; B, left mandible; C, maxillula; D, maxilla; E, maxilliped. Scale bar: 0.1 mm.

***Alpioniscus* (*Illyrionethes*) *drazinai* n. sp.**

(Figs 9–11, 15)

http://zoobank.org/80CE14BE-EE9C-4DD2-8978-3CFB267B4B0B

Alpioniscus (*Illyrionethes*) sp. 4.—Bedek *et al.* 2019: figs 3, 5.

Material examined. Croatia, Dalmatia, Dugi otok Island: ***Holotype*** male, Luka, Kamiškarta, Strašna peć (cave CCC HR00563), 44.0048°N, 15.0386°E, 29 July 2011, leg. J. Bedek (CBSSC IT4298).

FIGURE 7. *Alpioniscus* (*Illyrionethes*) *lossinii* **n. sp.** Paratype male CBSSC IT2379 from Medvjeđa špilja. A, pereopod 1 with enlargment of dactylus; B, pereopod 7 rostral view with enlargement of merus ; C, pereopod 7 merus caudal view with enlargment of hook. Scale bars: A, B = 1 mm; C, = 0.1 mm.

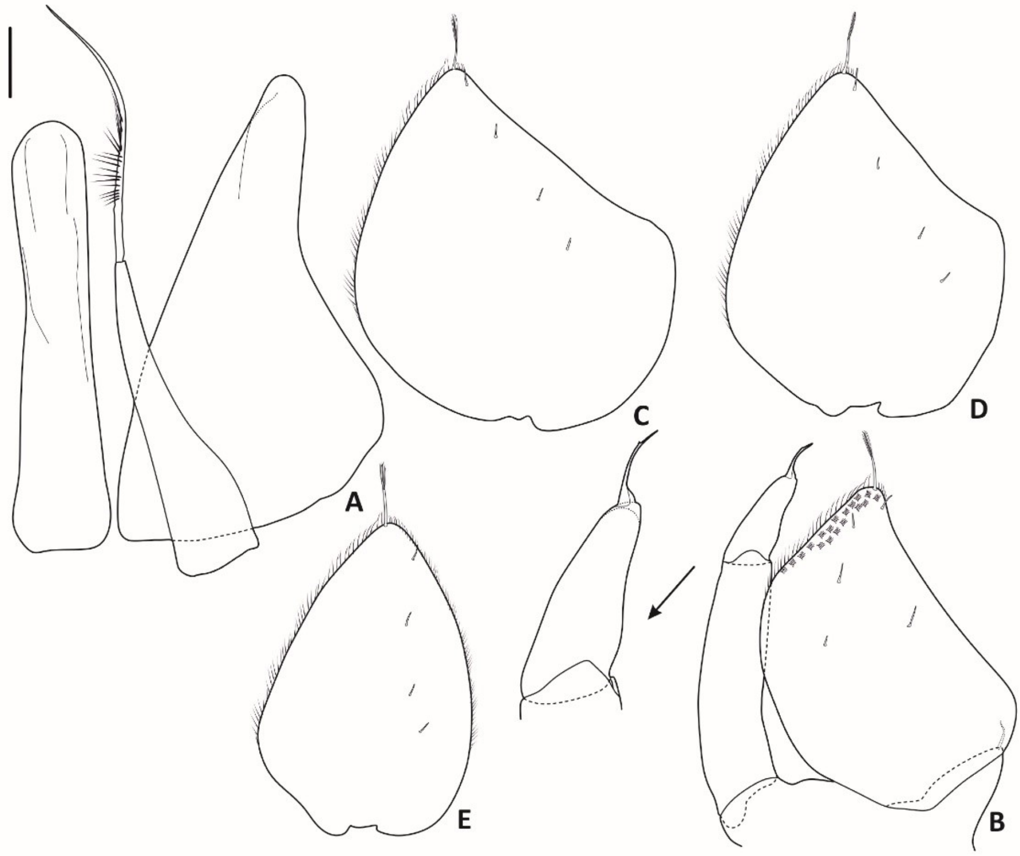

FIGURE 8. *Alpioniscus* (*Illyrionethes*) *lossinii* **n. sp.** Paratype male CBSSC IT2379 from Medvjeđa špilja. A, genital papilla and pleopod 1; B, pleopod 2 with enlargement of endopod tip; C, pleopod 3 exopod; D, pleopod 4 exopod; E, pleopod 5 exopod. Scale bar: 0.1 mm.

Paratypes. 1 male, 14 females, sama data as holotype, (CBSSC IT2390); 1 male, same locality and date, leg. J. Bedek, T. Dražina (CBSSC IT2391); 1 male, 2 females, same locality, 11 October 2003, leg. J. Bedek (MZUF 9845); 1 male, 3 females, same locality and date, leg. B. Jalžić (CBSSC IT279); 4 females, 2 females juv., same locality, 30 September 2006, leg. H. Bilandžija (CBSSC IT4229); 1 male, Sali, Ćirova jama (cave), 43.9250°N, 15.1674°E, 9 May 2017, leg. K. Cindrić (CBSSC IT4207); 3 males, 5 females, 3 juvs, Sali, Jamnjak, Jama na Jamnjaku (cave), 43.9396°N, 15.1461°E, 5 May 2002, leg. A. Katalinić, T. Dražina, M. Lukić, J. Bedek, A. Sudar, H. Bilandžija, L. Katušić (CBSSC IT4234); 2 males, 2 females, 1 juv., same locality, 25 September 2017, leg. K. Cindrić (CBSSC IT4204); 2 males, 3 females, Sali, Čušćica, Jama u Čuščici (cave), 43.8990°N, 15.2121°E, 2 May 2002, leg. A. Katalinić, T. Dražina, M. Lukić, J. Bedek, A. Sudar, H. Bilandžija, L. Katušić (CBSSC IT4232); 1 male, 2 females, 1 juv., same locality, 9 May 2017, leg. L. Kauf (CBSSC IT4200); 1 male, 1 male juv., 2 females, 1 juv., same data (CBSSC IT4201); 1 male, same locality and date, leg. K. Cindrić (MZUF 9893); 2 males, 5 females, 1 juv., Žman, Slotnjak, Podslotnjak (cave), 43.9577°N, 15.1175°E, 29 September 2017, leg. T. Dražina (CBSSC IT4195); 1 male, 1 male juv., 3 females, same locality and date, leg. K. Cindrić (CBSSC IT4196); 2 males, 2 females, same locality, 11 May 2017, leg. T. Dražina (CBSSC IT4197); 1 female, same data (CBSSC IT4198); 1 male juv., 3 females, 2 juvs, same locality and date, leg. P. Novina (CBSSC IT4199).

Other material. **Croatia, Dalmatia, Kornati archipelago, Piškera Island:** 2 males, 1 male juv., 5 females, Blitvica (cave), 43.7652°N, 15.3526°E, 2 October 2017, leg. A. Kirin (CBSSC IT4141); 2 males, 1 female juv., same locality and date, leg. V. Sudar (CBSSC IT4144); 2 males, 3 females, same locality, 21 April 2018, leg.

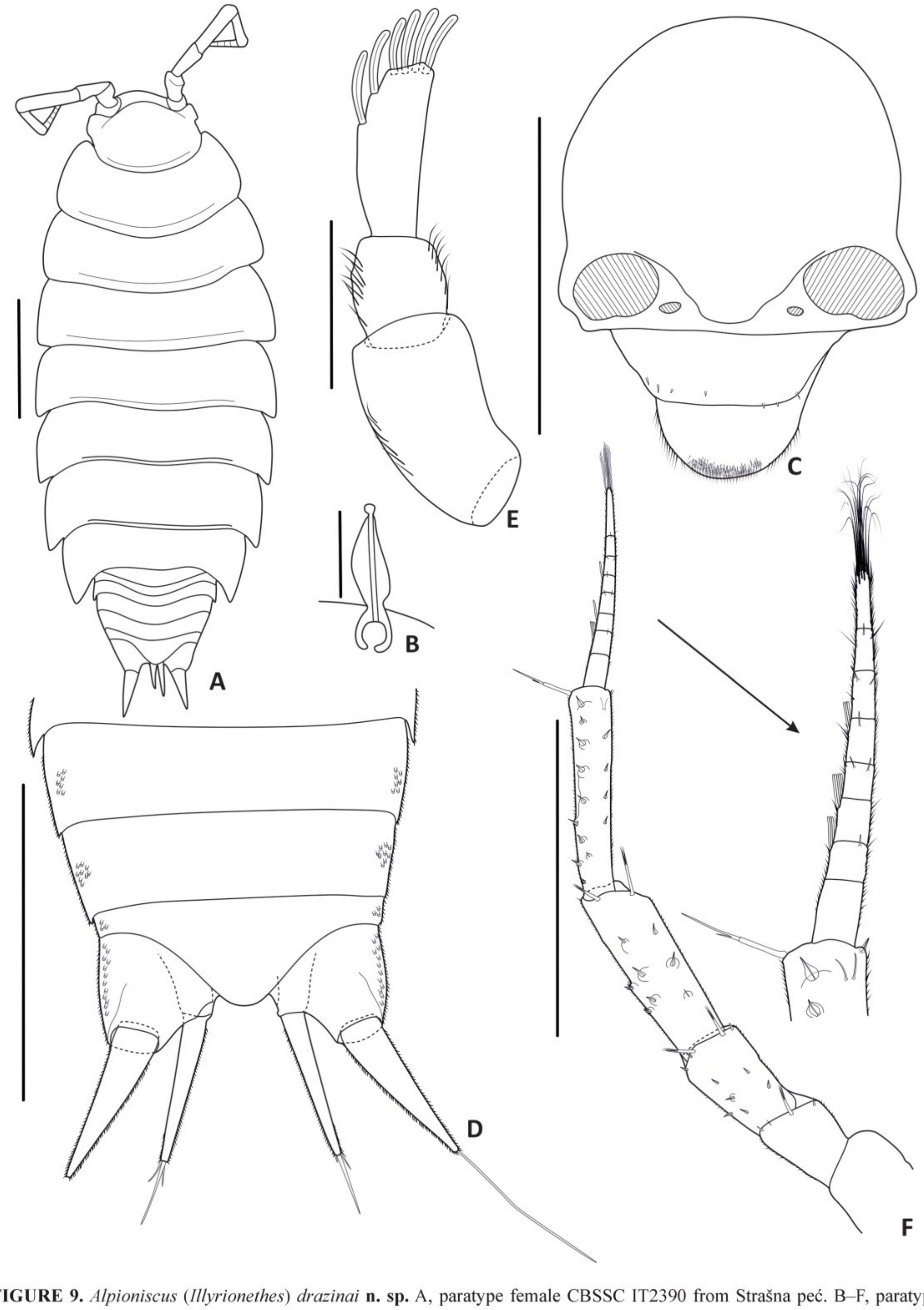

FIGURE 9. *Alpioniscus* (*Illyrionethes*) *drazinai* **n. sp.** A, paratype female CBSSC IT2390 from Strašna peć. B–F, paratype male CBSSC IT2390 from Strašna peć. A, specimen in dorsal view; B, dorsal scale-seta; C, cephalon, dorsal; D, pleonites 4, 5, telson and uropods; E, antennula; F, antenna with enlargment of flagellum. Scale bars: A, C, D, F = 1 mm; B = 0.01 mm; E = 0.1 mm.

T. Rožman (CBSSC IT4249); 1 female, Petra Stijene (cave), 43.7662°N, 15.3485°E, 2 October 2017, leg. L. Ružanović (CBSSC IT4124); 4 males, 4 females, same locality, 21 April 2018, leg. T. Čuković, H. Cvitanović (CBSSC IT4236); 1 female, same locality and date, leg. T. Čuković (CBSSC IT4237); 1 male, 1 female, same locality and date, leg. H. Cvitanović (CBSSC IT4240); 1 male, 4 females, same locality, 19 April 2018, leg. H. Cvitanović (CBSSC IT4241); 1 male, 1 female, same locality and date, leg. T. Rožman (CBSSC IT4243).

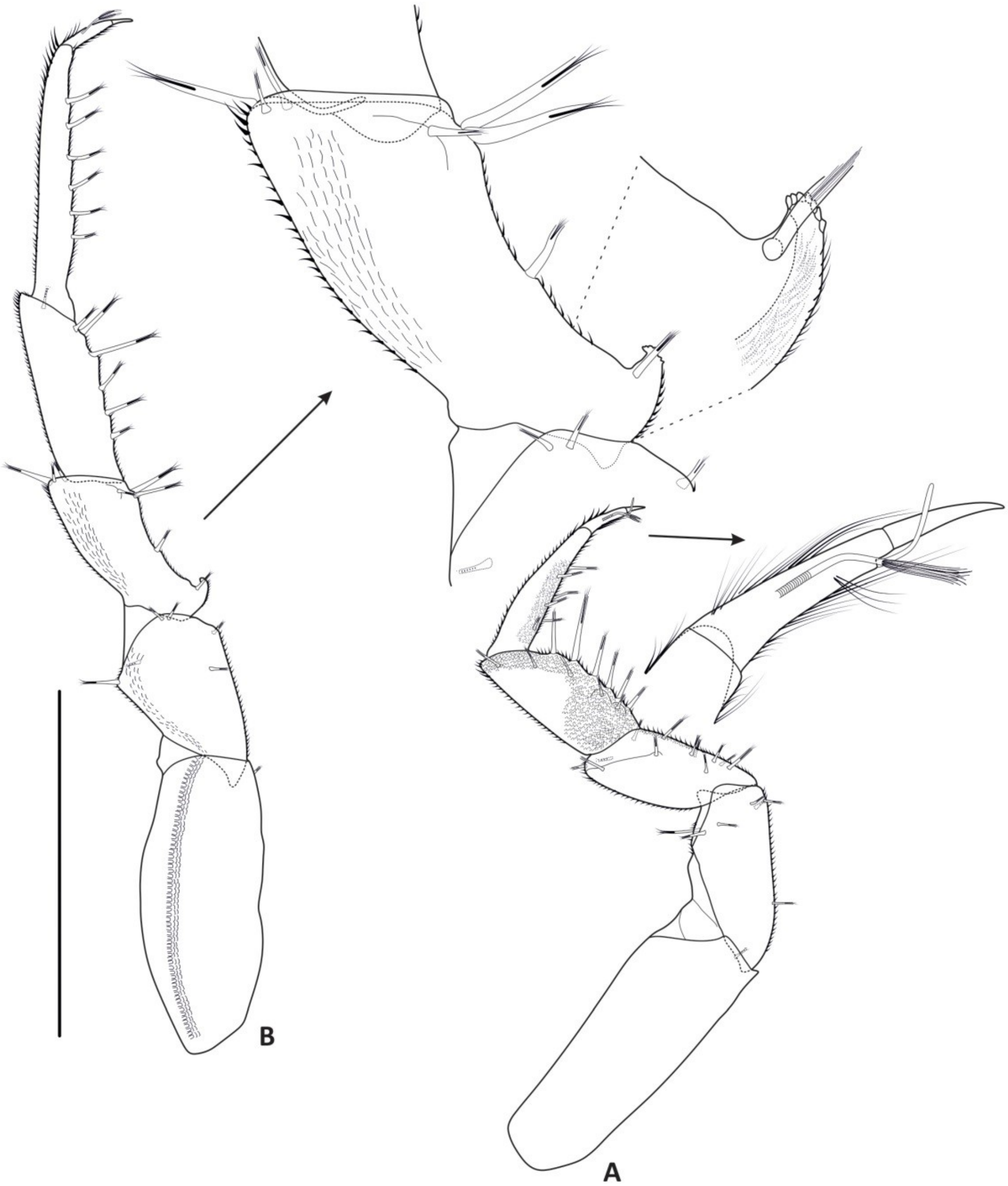

FIGURE 10. *Alpioniscus* (*Illyrionethes*) *drazinai* **n. sp.** Paratype male CBSSC IT2390 from Strašna peć. A, pereopod 1 with enlargment of dactylus ; B, pereopod 7 rostral view with enlargements of merus and hook. Scale bar: 1 mm.

Description. Maximum length: male, 5.2 mm; female, 6.4 mm. Colourless *body*, *pereon* with almost parallel sides, *pleon* narrower than pereon (Fig. 9A). Back smooth to slightly granulated, with ridges near posterior margins of cephalon and pereonites 1–6 (Fig. 9A), and some triangular scale-setae (Fig. 9B). Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods (Fig. 9D).

Cephalon (Fig. 9C) with suprantennal line bent down in middle; antennal lobes quadrangular, dorsally concave. *Eyes* absent. Posterior margin of pereonites 1, 2 convex, of pereonite 3 straight, and of pereonites 4–7 progressively more concave (Fig. 9A). Pleonites 3–5 with small posterior points visible in dorsal view (Fig. 9D). Distal part of telson with concave sides and rounded apex (Fig. 9D).

Antennula (Fig. 9E) of three articles, distal article flattened with five to eight aesthetascs. *Antenna* (Fig. 9F) with peduncle granulated; flagellum of eight to 10 articles with one row of aesthetascs on three to five different articles, always on second and third. *Buccal pieces* as in *A. magnus*.

Pereopods similar in shape, ungual seta simple, dactylar seta bifid and setose (Fig. 10A).

Uropod (Fig. 9D) with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male: *Pereopod 1* (Fig. 10A) carpus bearing five to seven setae. *Pereopod 1 and 2* with propodus and carpus bearing numerous short scales on rostral surface. *Pereopods 4–6* merus with small lobe proximally on sternal margin. *Pereopod 7* (Fig. 10B) ischium with straight sternal margin; merus with slightly concave sternal margin and large hook-shaped lobe bearing scales and one seta; carpus with straight sternal and tergal margins.

Genital papilla (Fig. 11A) with rounded apical part.

Pleopod 1 (Fig. 11A) exopod with thickset subquadrangular distal part, apex broadly rounded, sinuous outer margin, slightly convex inner margin; endopod triangular, narrow, armed with long apical plumose seta.

Pleopod 2 (Fig. 11B) exopod triangular with slightly concave outer margin and apical seta; endopod of two articles, distinctly longer than exopod, distal article with posterior part narrower with strong seta subapically bifid.

Pleopod 3–5 exopods as in *A. lossinii*.

Etymology. The new species is named after Dr. Tvrtko Dražina, team coordinator of the Dugi otok biospeleological research.

Remarks. *Alpioniscus drazinai* **n. sp.** differs from all the other species lacking a tergal hump on the male pereopod 7 carpus by the subquadrangular distal part of the male pleopod 1 exopod and the large and protruding hook on the male pereopod 7 merus.

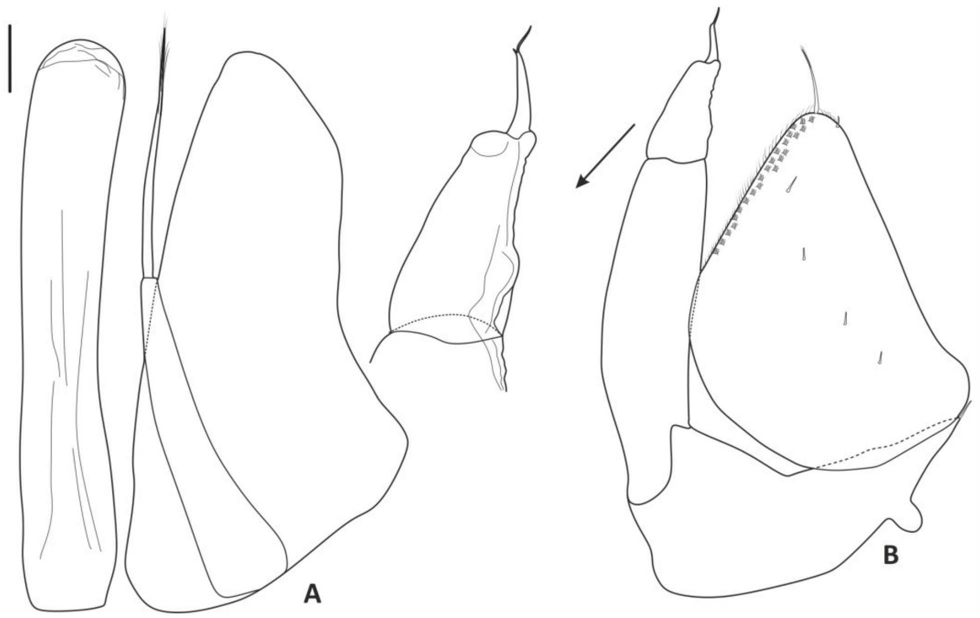

FIGURE 11. *Alpioniscus* (*Illyrionethes*) *drazinai* **n. sp.** Paratype male CBSSC IT2390 from Strašna peć. A, genital papilla and pleopod 1; B, pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

***Alpioniscus (Illyrionethes) mandalinae* n. sp.**
(Figs 12–15)
http://zoobank.org/83BC3A4A-3D1B-4CE8-9726-A80D9DD77919

Alpioniscus (*Illyrionethes*) sp. 5.—Bedek *et al.* 2019: figs 3, 5.

Material examined. Croatia, Dalmatia: ***Holotype*** male, Šibenik, Mandalina, Mandalina (cave CCC HR00247), 43.7111°N, 15.9021°E, 19 October 2012, leg. J. Bedek (CBSSC IT4297).

Paratypes. 1 female, 1 juv., same data as holotype (CBSSC IT2860); 1 female, same locality and date, leg. K. Miculinić (CBSSC IT2861); 1 male juv., same locality, 13 February 1998, leg. S. Vujčić-Karlo; 1 male, 5 females, same locality, 15 January 2002, leg. B. Jalžić (CBSSC IT270); 2 females, same locality, 6 October 2005, leg. M. Lukić (CBSSC IT319); 5 females, same locality and date, leg. J. Bedek (CBSSC IT320); 2 females, same locality and date, leg. R. Ozimec (CBSSC IT3027); 6 females, 1 juv., same locality and date, leg. M. Pavlek (CBSSC IT4001); 5 males, 7 females, same locality, 8 May 2010, leg. A. Kirin (CBSSC IT2166); 2 females, same locality and date, leg. J. Bedek (CBSSC IT2168); 1 female, same locality and date, leg. P. Kovač-Konrad (CBSSC IT2173); 3 females, same locality and date, leg. M. Lukić (CBSSC IT2174); 3 males, 3 females, 2 juvs, same locality, 14 December 2014, leg. P. Kutleša (MZUF 9844); 2 males, 6 females, 2 juvs, same locality and date, leg. J. Bedek (CBSSC IT3998); 2 males juv., 15 females, same data (CBSSC IT4006); 1 male, 17 females, 2 juvs, same locality, 5 March 2015, leg. J. Bedek (CBSSC IT3996); 2 males, 18 females, same locality, 10 October 2016, leg. J. Bedek (CBSSC IT3997).

Description. Maximum length: male, 3.5 mm; female, 6.3 mm. Colourless *body*, *pereon* with almost parallel sides, *pleon* narrower than pereon (Fig. 12A). Back smooth to slightly granulated, with ridges near posterior margins of cephalon and pereonites 1–6, and some triangular scale-setae (Fig. 12B). Some gland pores on lateral margins of pleonites 4 and 5 (Fig. 12C).

Cephalon (Fig. 12C) with suprantennal line bent downwards; antennal lobes rounded. Eyes absent. Posterior margin of pereonites 1, 2 convex, of pereonite 3 slightly convex, and of pereonites 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view (Fig. 12D). Distal part of telson with concave sides and broadly rounded apex (Fig. 12D).

Antennula (Fig. 12E) of three articles, distal article flattened with six to eight aesthetascs. Antenna (Fig. 12F) with peduncle granulated; flagellum of eight to 10 articles with one row of aesthetascs on four to five different articles, always on second and third. *Buccal pieces* as in *A. magnus*.

Pereopods similar in shape, ungual seta simple, dactylar seta bifid and setose (Fig. 13A).

Uropod (Fig. 12D) with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male: *Pereopod 1* (Fig. 13A) carpus bearing five setae. *Pereopod 1* and *2* propodus and carpus bearing numerous short scales on rostral surface; merus with sternal margin straight, *pereopods 3–6* merus with progressively more concave sternal margin and small lobe proximally. *Pereopod 7* (Fig. 13B) ischium with straight sternal margin; merus with slightly concave sternal margin and hook-shaped lobe proximally, with scales and one large seta; carpus with straight sternal and tergal margins.

Genital papilla (Fig. 14A) with rounded apical part.

Pleopod 1 (Fig. 14A) exopod triangular, wide, with rounded apex, almost straight outer margin, convex inner margin; endopod narrow with wide basal part and concave outer margin, with apical seta distinctly shorter than basal article.

Pleopod 2 (Fig. 14B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, distal article proximally narrower with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. lossinii*.

Etymology. The new species is named after Mandalina, name of the cave and peninsula where the specimens were collected.

Remarks. *Alpioniscus mandalinae* differs from all the other species lacking a tergal hump on the male pereopod 7 carpus by the wide male pleopod 1 exopod with almost straight outer margin.

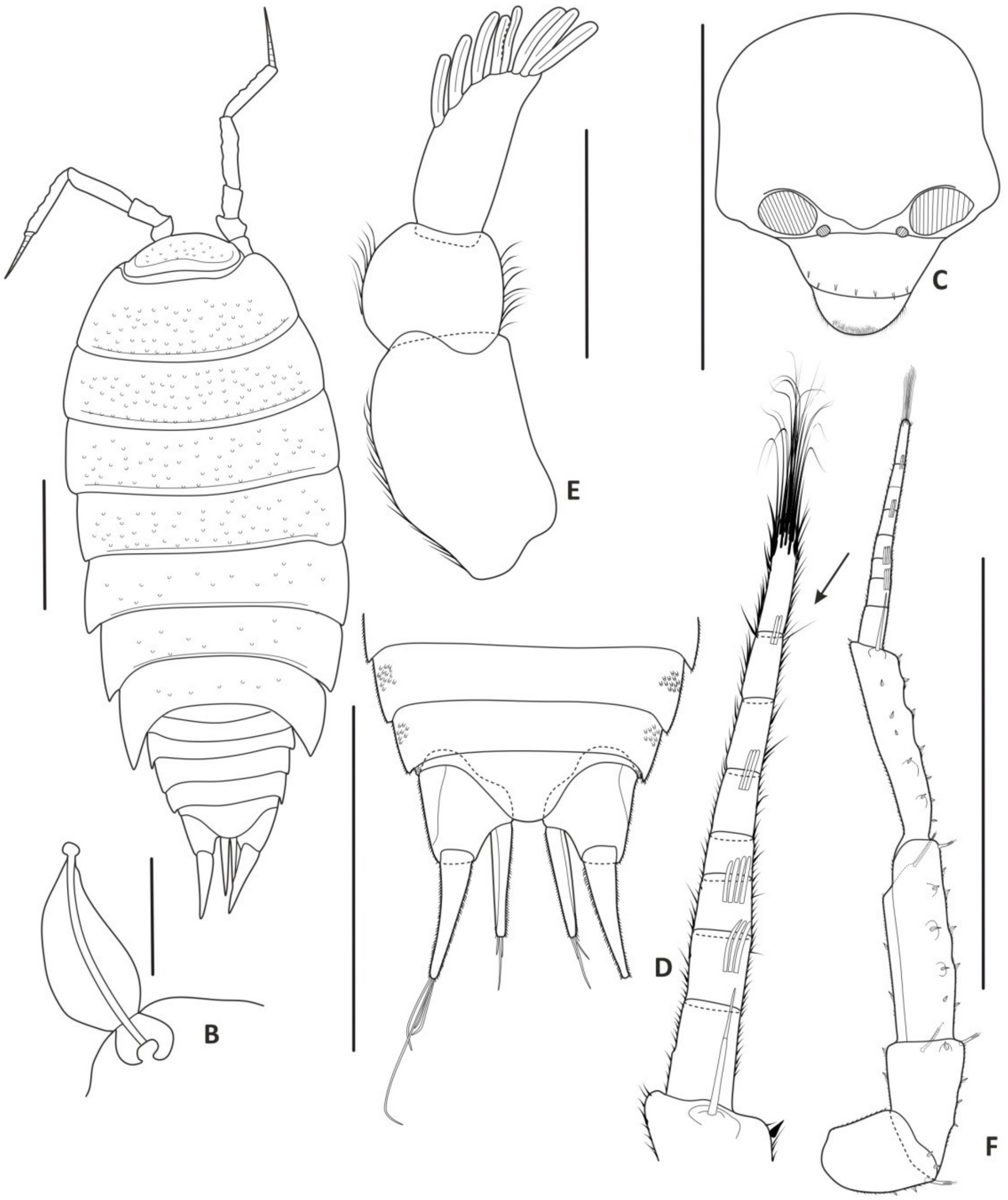

FIGURE 12. *Alpioniscus* (*Illyrionethes*) *mandalinae* **n. sp.** A, paratype female CBSSC IT4001 from Mandalina. B–D, paratype male CBSSC IT2166 from Mandalina. E, F, paratype male CBSSC IT3997 from Mandalina. A, specimen in dorsal view; B, dorsal scale-seta seta; C, cephalon, dorsal; D, pleonites 4, 5, telson and uropods; E, antennula; F, antenna with enlargment of flagellum. Scale bars: A, C, D, F = 1 mm; B = 0.01 mm; E, 0.1 mm.

Discussion

With the three new species described here, the number of nominal species of *Illyrionethes* from the Dinaric Karst is now 18. According to the molecular analysis using large ribosomal subunit 16S (Bedek *et al.* 2019), the *magnus*-lineage is the sister group of the *heroldi*-lineage, which is in agreement with preliminary taxonomical analyses by Bedek & Taiti (2011). The four species of the *magnus*-lineage have disjunct distributions in the coastal part of Croatia (Fig. 15): *A. magnus* is endemic to Brač island, *A. lossinii* to Mali Lošinj island, *A. drazinai* to Dugi otok island and Kornati archipelago, and *A. mandalinae* to Šibenik coastal area. Among this group of species, only *A. magnus* has an amphibious behaviour, while all the others have never been collected in water.

FIGURE 13. *Alpioniscus* (*Illyrionethes*) *mandalinae* **n. sp.** Paratype male CBSSC IT3997 from Mandalina. A, pereopod 1 with enlargment of dactylus; B, pereopod 7 rostral view with enlargements of merus and hook. Scale bar: 1 mm.

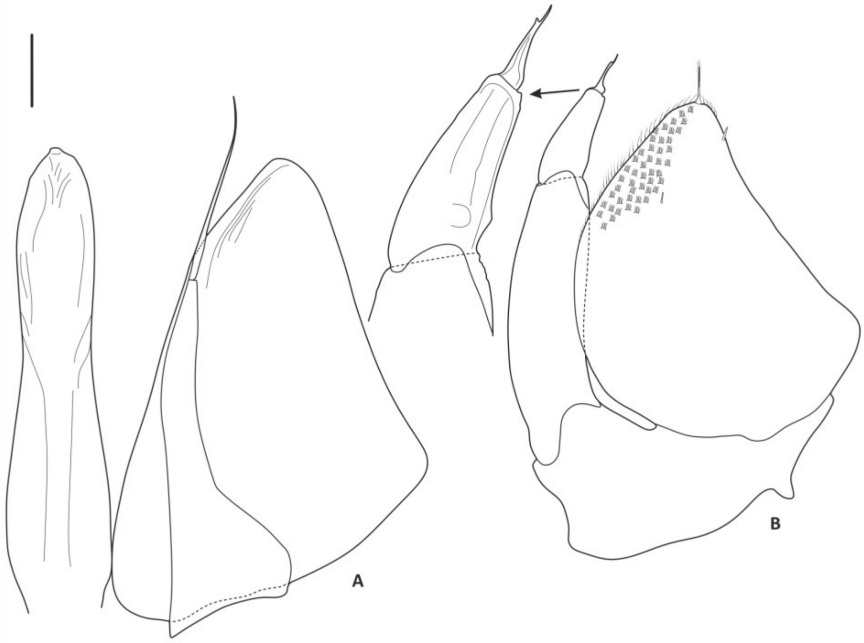

FIGURE 14. *Alpioniscus* (*Illyrionethes*) *mandalinae* **n. sp.** Paratype male CBSSC IT3997 from Mandalina. A, genital papilla and pleopod 1; B, pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

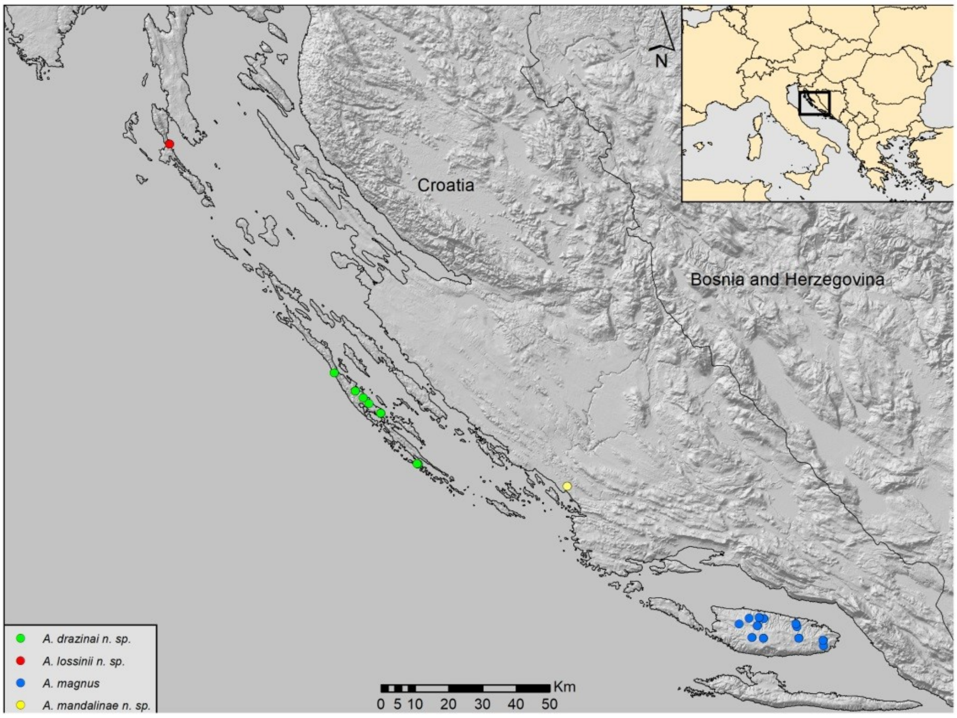

FIGURE 15. Distribution map of analysed specimens of the *Alpioniscus* species, *magnus*-lineage in Croatia.

Acknowledgements

The authors are grateful to all collectors and the (bio)speleologists from the Croatian Biospeleological Society, Biological Students Society BIUS, Speleological Section of the Croatian Mountaineering Club Željezničar and Speleological Section of the Mountaineering Society Profunda for helping with the fieldwork. Dr. Josip Balabanić is particularly acknowledged for reviewing the new species names. The anonymous referees improved the manuscript with valuable comments and suggestions. The majority of examined specimens were collected through different projects conducted by the Croatian Biospeleological Society and partly supported by the National Park Krka; National Park Kornati; Nature Park Telašćica; Public Institute for the Management of Protected Natural Areas and Other Protected Natural Areas in Šibenik-Knin County; The Environmental Protection and Energy Efficiency Fund, Croatia (project leaders Branko Jalžić, Tvrtko Dražina, Ana Komerički, Kazimir Miculinić, Tamara Čuković and Petra Kutleša).

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Paper 4

Bedek J, Gottstein S, Taiti S (2019) A new species of *Alpioniscus* (*Illyrionethes*) from the Dinaric Karst (Isopoda, Oniscidea, Trichoniscidae). Subterranean Biology 32: 33–42. https://doi.org/10.3897/subtbiol.32.37509

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RESEARCH ARTICLE

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A new species of *Alpioniscus* (*Illyrionethes*) from the Dinaric Karst (Isopoda, Oniscidea, Trichoniscidae)

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Abstract

In the Dinaric Karst, *Alpioniscus* (*Illyrionethes*) is the taxon with the largest number of troglobiotic species (19), one of which is new and described here: *A. busljetai* **sp. nov.**, found in two caves in the coastal area of North Dalmatia. Both caves are threatened by human activities (IUCN threats 1.1, 9.1.1).

Keywords

Adriatic coast, cave fauna, new species, terrestrial isopods, Trichoniscinae, troglobiotic

Introduction

Alpioniscus Racovitza, 1908 is the most abundant and widespread terrestrial isopod genus in caves of the Dinaric Karst. It is represented by the subgenus *Illyrionethes* Verhoeff, 1927, with a range from Trieste in Italy to Durmitor in Montenegro (Schmalfuss 2003, Horvatović 2014). This subgenus is present also with six endogean, troglobiotic and stygobiotic species in Sardinia, Italy (Taiti et al. 2018). A recent integrative taxonomic study of *Illyrionethes* species from the Dinaric Karst revealed 19 troglobiotic species, one of which remained undescribed (Bedek et al. 2017; Bedek et al. 2019; in press). They grouped into three different lineages (*strasseri-*, *heroldi-* and *magnus*-lineage), with overlapping ranges. Nine species are restricted to coastal areas with limited distribution ranges: *A. christiani* (Potočnik, 1983) from the *strasseri*-lineage; *A. magnus* (Frankenberger, 1938), *A. lossinii* Bedek, Gottstein & Taiti, 2019, *A. drazinai* Bedek, Gottstein & Taiti, 2019, and *A. mandalinae* Bedek, Gottstein & Taiti, 2019 from the *magnus*-lineage; *A. trogirensis* Buturović, 1955, *A. kratochvili* (Frankenberger, 1938), *A. haasi* (Verhoeff, 1931) and the new species described below from the *heroldi*-lineage.

Material and methods

Specimens were hand collected with tweezers, fixed and stored in 75% ethanol with glycerol or 96% ethanol. Several specimens were dissected and mounted for micropreparations in Hoyer's medium (Anderson 1954). For identifications and illustrations in the description, the entire body and the following appendages were used: antennae, antennulae, buccal pieces, male pereopods 1 and 7, genital papilla and male pleopods 1 and 2. Specimens were examined under a Zeiss Stemi 2000-C, Zeiss Primo Star and Nikon Labophot microscopes. Micropreparations were photographed using Canon EOS 40D and EOS Utility software. Drawings were made from photographs. The examined material, description, etymology and remarks are given. The following numerical characters were counted: the number of (1) antennular aesthetascs, (2) antennal flagellum articles, (3) antennal flagellum articles bearing aesthetascs, and (4) setae on the male pereopod 1 carpus. The terminology used in species description is mainly based on Vandel (1960, 1962). The locality coordinates used the WGS84 datum. The map was drawn using ArcMap 10.1 software and related Shadow Relief layer. The IUCN threats are determined according to the Classification Schemes used in IUCN Red List assessments (IUCN 2012).

Repositories:

CBSSC Croatian Biospeleological Society Collection, Zagreb, Croatia
MZUF Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia La Specola, Florence, Italy

Taxonomy

Family Trichoniscidae Sars, 1899
Subfamily Trichoniscinae Sars, 1899
Genus *Alpioniscus* Racovitza, 1908
Subgenus *Illyrionethes* Verhoeff, 1927

***Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov.**
http://zoobank.org/F48F1286-A661-4B19-AC7E-3B37FC333E53
Figs 1–6

Alpioniscus sp. – Bregović et al. 2008: 109 [partim: Markova špilja].
Alpioniscus (*Illyrionethes*) sp. 3. – Bedek et al. in press: figs 3, 5.

Material examined. Holotype: ♂ Croatia, Starigrad Paklenica, Seline, Markova špilja (cave), 44°16.79'N, 15°28.63'E, 30.IX.2008, D. Hmura leg., CBSSC IT4252. **Paratypes:** 1 ♂, 1 ♀, 1 juv., same data as holotype, CBSSC IT2407; 1 ♀, 1 juv., ibid., 5.VI.2006, H. Bilandžija leg., CBSSC IT560; 2 ♂♂, 1 ♀, ibid., 5.VI.2006, M. Pavlek leg., CBSSC IT561; 2 ♂♂, 2 ♀♀, ibid., 1.V.2010, A. Kirin leg., CBSSC IT2235; 1 ♂ juv., ibid., 1.V.2010, M. Lukić leg., CBSSC IT3975; 1 ♂ juv., ibid., 18.XII.2012, A. Komerički leg., CBSSC IT2881; 1 ♀, ibid., 18.III.2013, K. Miculinić leg., CBSSC IT3974; 1 ♂, 1 ♀, 1 juv., ibid., 20.V.2018, P. Bregović leg., MZUF 9894; 3 ♂♂, 4 ♀♀, ibid., 20.V.2018, N. Kuharić leg., CBSSC IT4250; 2 ♀♀, ibid., 20.V.2018, N. Kuharić leg., CBSSC IT4398; 2 ♀♀, ibid., 20.V.2018, I. Jaklinović leg., CBSSC IT4251; 2 ♀♀, 1 juv., ibid., 20.V.2018, M. Čuček leg., CBSSC IT4399; 2 ♂♂, 1 ♂ juv., 2 ♀♀, Croatia, Starigrad Paklenica, Špecina špajza (cave), 44°17.10'N, 15°27.46'E, 29.VI.2013, A. Komerički leg., CBSSC IT3960; 2 ♀♀, ibid., 29.VI.2013, T. Dražina leg., CBSSC IT3961; 1 ♂, 1 ♀, ibid., 29.VI.2013, T. Dražina leg., CBSSC IT3962.

Figure 1. *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov. *in situ* in Markova špilja (by courtesy of Petra Kutleša). Scale bar: 1 mm.

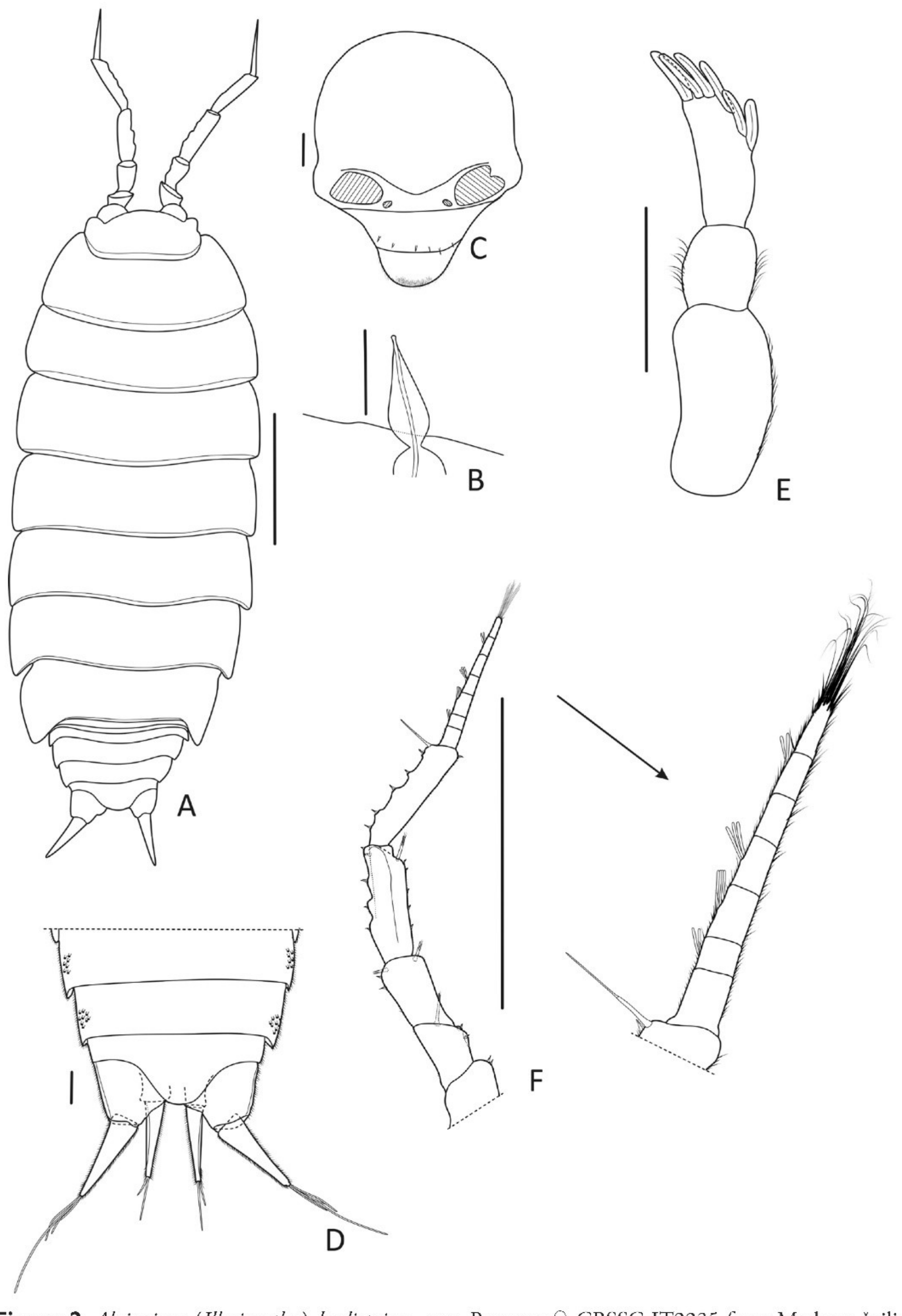

Figure 2. *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov. Paratype ♀ CBSSC IT2235 from Markova špilja **A** habitus in dorsal view. Paratype ♂ CBSSC IT2235 from Markova špilja **B** dorsal scale-seta **C** cephalon, dorsal **D** pleonites 4, 5, telson and uropods. Paratype ♂ CBSSC IT4250 from Markova špilja **E** antennula **F** antenna with enlargement of flagellum. Scale bars: 1 mm (**A, F**), 0.1 mm (**C–E**), 0.01 mm (**B**).

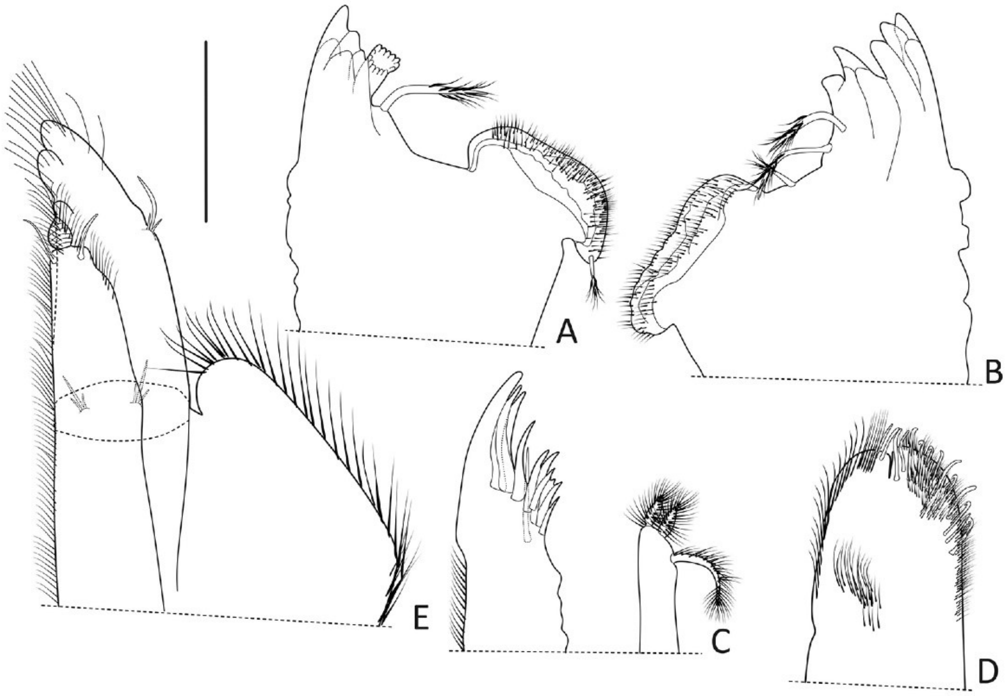

Figure 3. *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov. Paratype ♂ CBSSC IT2235 from Markova špilja **A** right mandible **B** left mandible **C** maxillula **D** maxilla **E** maxilliped. Scale bar: 0.1 mm.

Description. Maximum length: ♂, 4.4 mm; ♀, 6.0 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon (Figs 1, 2A). Back smooth, with ridges near posterior margins of cephalon and pereonites, and some triangular scale-setae (Fig. 2B). Some gland pores on lateral margins of pleonites 4 and 5 (Fig. 2D). Eyes absent. Cephalon (Fig. 2C) with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and of pereonites 4–7 progressively more concave (Fig. 2A). Pleonites 3–5 with small posterior points visible in dorsal view (Fig. 2D). Distal part of telson with concave sides and broadly rounded apex (Fig. 2D). Antennula (Fig. 2E) of three articles, distal article flattened and bearing five to six aesthetascs. Antenna (Fig. 2F) with distal articles of peduncle granulated; flagellum of five to seven articles with one row of aesthetascs on two to four different articles, always on second and third. Mandibles (Fig. 3A, B) with one penicil in right and three in left; molar process with one penicil in right and none in left. Outer branch of maxillula (Fig. 3C) with 4+6 teeth, apically entire, and one slender stalk; inner branch with three penicils, outer and middle subequal, inner distinctly longer. Maxilla (Fig. 3D) with setose and bilobate apex, lobes subequal in width. Maxilliped (Fig. 3E) endite narrow, with large segmented apical penicil; palp distally with three rounded lobes, basal article with two small compound setae; basis with rounded outer lobe protruding posteriorly and covered with long setae on margin. Pereopods with large, bifid and setose dactylar seta (Fig. 4A). Uropod (Fig. 2D)

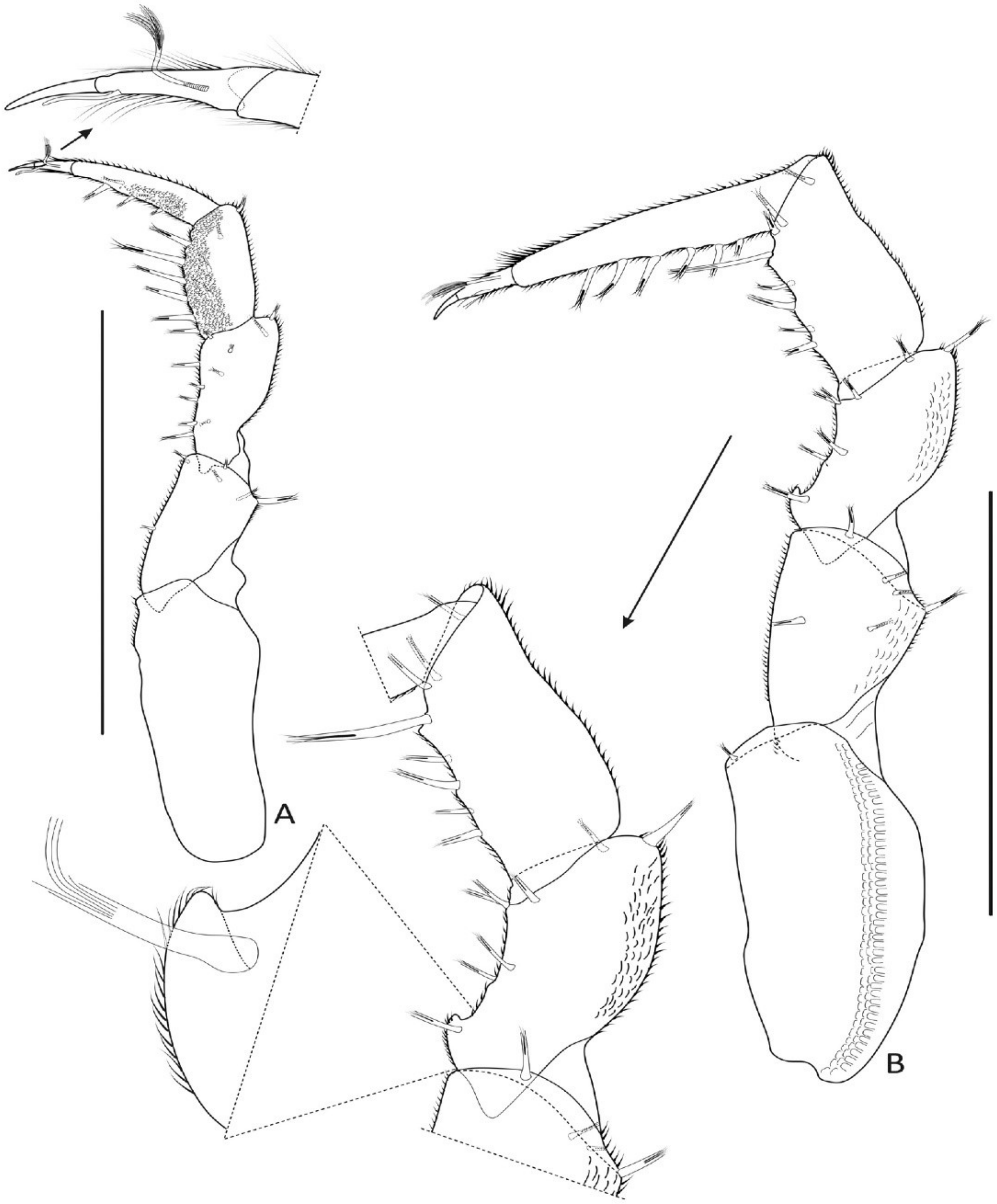

Figure 4. *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov. Paratype ♂ IT4250 from Markova špilja **A** pereopod 1 with enlargement of dactylus **B** pereopod 7 rostral view with enlargement of carpus and merus, and merus hook. Scale bars: 1 mm.

with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male. Pereopod 1 (Fig. 4A) carpus bearing four to six setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods

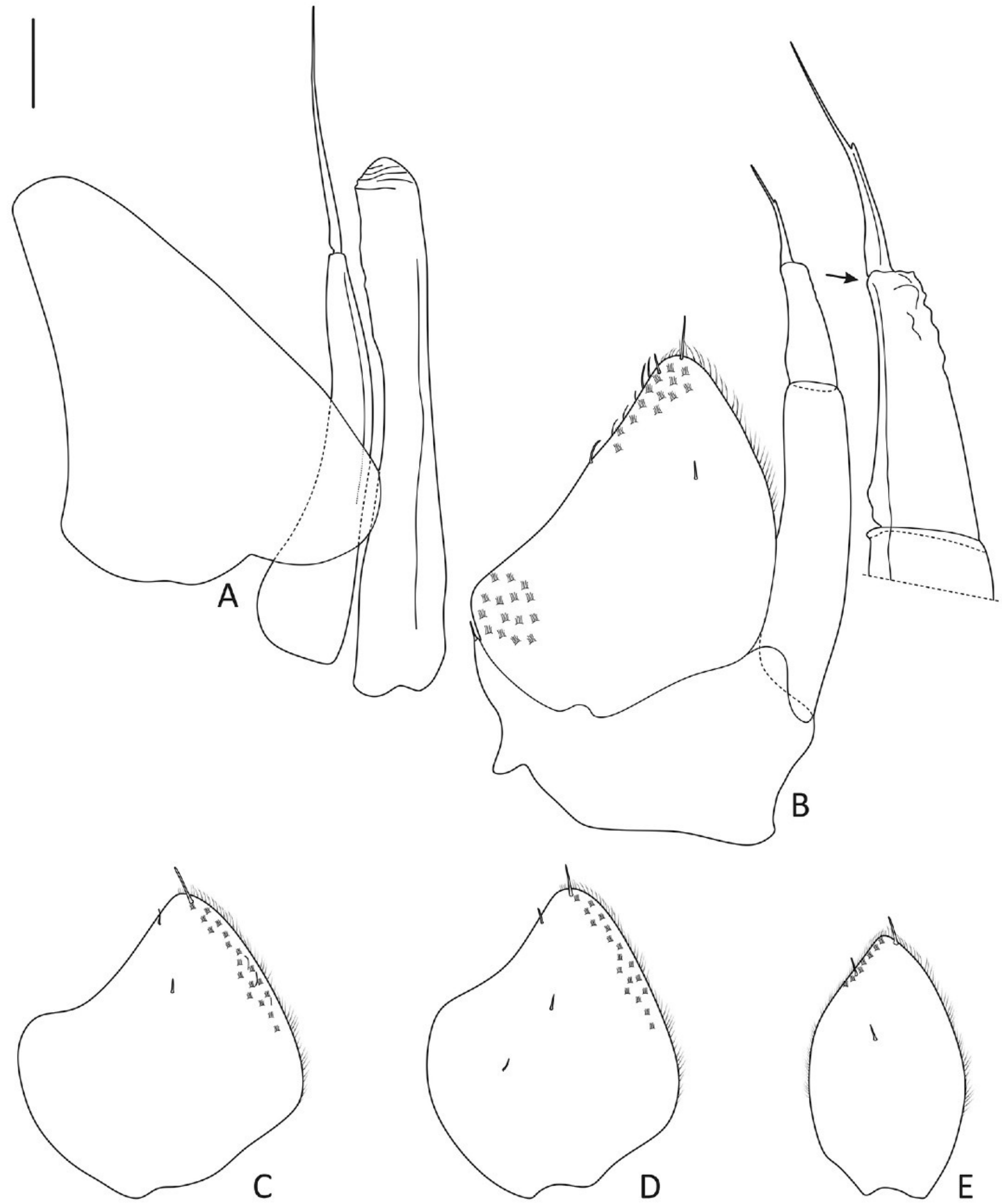

Figure 5. *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov. Paratype ♂ IT4250 from Markova špilja **A** genital papilla and pleopod 1 **B** pleopod 2 with enlargement of endopod tip. Paratype ♂ CBSSC IT2235 from Markova špilja **C** pleopod 3 exopod **D** pleopod 4 exopod **E** pleopod 5 exopod. Scale bar: 0.1 mm.

1–4 merus with sternal margin straight, pereopods 5, 6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Fig. 4B) ischium with straight sternal margin; merus with slightly concave sternal margin and small hook-shaped lobe in proximal part directed ventro-laterally and bearing one seta; carpus with

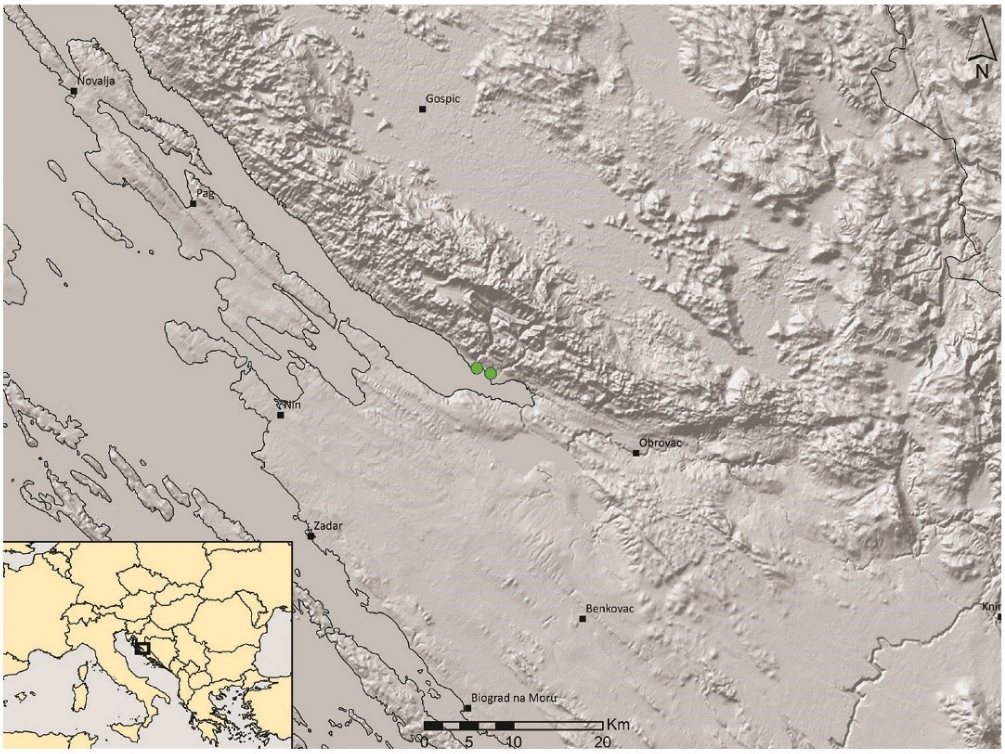

Figure 6. Distribution map of *Alpioniscus* (*Illyrionethes*) *busljetai* sp. nov.

straight sternal margin and shallow and long rounded tergal hump in proximal part. Genital papilla (Fig. 5A) with rounded apical part. Pleopod 1 (Fig. 5A) exopod with posterior apex broadly rounded, slightly concave outer margin, straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Fig. 5B) exopod triangular with concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in Fig. 5C–E.

Etymology. The species is named after Dujo Bušljeta, the National park Paklenica ranger and Croatian Biospeleological Society field research guide within the Paklenica area.

Remarks. *Alpioniscus busljetai* sp. nov. differs from Dinaric *Illyrionethes* species by the shallow and long rounded tergal hump of the male pereopod 7 carpus, similar to the one present only in *A. trogirensis*. It differs from *A. trogirensis* in the shape of the male pleopod 1 exopod, with broadly rounded posterior apex and slightly concave outer margin (narrowly rounded posterior apex and sinuous outer margin in *A. trogirensis*). The shape of the male pleopod 1 exopod is similar to the one of *A. tuberculatus* (Frankenberger, 1939), from which it differs by the presence of the dorsal hump of the male pereopod 7 carpus and smooth habitus.

Discussion

Alpioniscus busljetai sp. nov. belongs to the *heroldi*-lineage according to the molecular analysis and to the slightly concave outer margin of the male pleopod 1 exopod, a character in common also with the species of the *magnus*-lineage (Bedek et al. in press).

The majority of Dinaric *Illyrionethes* species are not particularly endangered (Ozimec et al. 2009). About half species are restricted to a relatively small, usually coastal, area, and five species are known from a single or just two caves. *Alpioniscus busljetai* sp. nov. is found in only two caves in the coastal area of the Velebit Mt., North Dalmatia. Both caves are located in a rural area, with strong potential for tourism growth. Markova špilja is a small, anchialine cave, in the vicinity of houses at the end of the village Seline. Further growth of the village represents the potential risk of a negative impact on the cave or even its destruction (IUCN threat 1.1). Špecina špajza is a small cave with a cave lake, placed among houses in the village Starigrad Paklenica. The human impact on the cave is already present, by housing waste water (IUCN threat 9.1.1) and because the entrance to the cave has been completely destroyed due to construction work (IUCN threat 1.1) (Ana Komerički and Tvrtko Dražina pers. com.).

All the narrow endemics of *Alpioniscus* in the Dinaric Karst are facing or already have been threatened by human activities due to the high urbanisation of the Adriatic coast. The cave fauna inventory and taxonomic analyses are still fundamental for the conservation of the cave biodiversity in the Dinaric Karst.

Acknowledgments

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DISCUSSION

The integrative taxonomical study confirmed 12 out of 13 nominal and seven out of 12 putative undescribed species. The existence of the three nominal subspecies was inconclusive within the study. The nominal species, *A. bosniensis* is considered to be a junior synonym of *A. heroldi*, based on molecular and morphological analyses. The remaining 5 putative undescribed species were not analysed in the frame of this study, due to unavailability of freshly collected material for molecular studies. With seven new species described (*A. iapodicus* Bedek, Horvatović and Karaman, 2017, *A. hirci* Bedek & Taiti, 2019, *A. velebiticus* Bedek & Taiti, 2019, *A. lossinii* Bedek, Gottstein and Taiti, 2019, *A. drazinai* Bedek, Gottstein and Taiti, 2019, *A. mandalinae* Bedek, Gottstein and Taiti, 2019 and *A. busljetai* Bedek, Gottstein and Taiti, 2019) the Dinaric *Illyrionethes* comprises at the moment 19 nominal and five putative undescribed species.

Molecular analyses

Analysed Dinaric *Illyrionethes* were grouped in three lineages: *heroldi*-, *strasseri*- and *magnus*-lineage with Maximum Likelihood (ML) and Bayesian Inference (BI) of large ribosomal subunit 16S (16S) analyses. The inclusion of the nuclear histone H3 marker caused dispersal of the *magnus*-lineage throughout the tree, therefore *magnus*-lineage is considered as tentative. Nine species are included in the *heroldi*-lineage (Figure 2, Figure 3): *A. heroldi, A. haasi, A. kratochvili, A. absoloni, A. trogirensis*, *A. verhoeffi*, *A. tuberculatus, A. herzegowinensis,* and *A. busljetai*. The *strasseri*-lineage encompasses six species (Figure 4, Figure 5): *A. strasseri; A. balthasari, A. christiani, A. hirci,* and *A. velebiticus*. The *magnus*-lineage includes four species (Figure 6, Figure 7): *A. magnus, A. lossinii, A. drazinai,* and *A. mandalinae*. The molecular analyses of the *strasseri*-lineage revealed lower cytochrome oxidase I (COI) and 16S interspecific distances as well as later divergence times compared to the *heroldi*- and *magnus*-lineage.

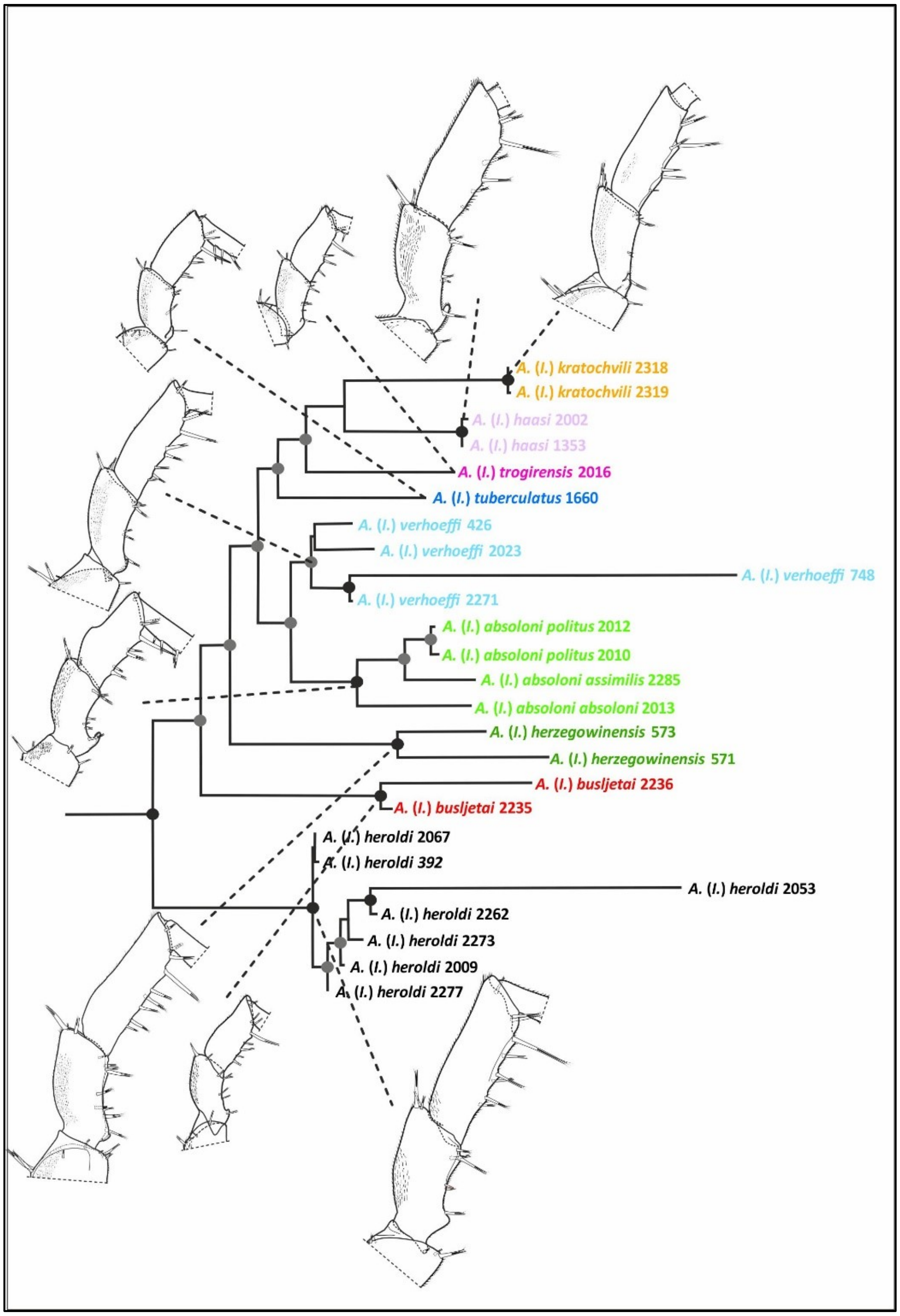

Figure 2. *Alpioniscus* (*Illyrionethes*), the *heroldi*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pereopod 7 carpus and merus of the *heroldi*-lineage. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Partly adapted from Bedek *et al.* 2019a and 2019c, with permission.

The minimum interspecific distances in this study are for COI 12% and for 16S 5%, which is similar to other research of Oniscidea (from 13 for COI and 7.6 for 16S) (Klossa-Kilia et al. 2006; Sicard et al. 2014; Zimmermann et al. 2015).

The three major lineages of Dinaric *Illyrionethes* split ~10–9 Myr ago, while speciations occurred from ~10-2 Myr ago. These results are concordant with other Oniscidea estimations of divergence times between different taxa (Poulakakis and Sfenthourakis 2008; Dimitriou et al. 2018). The separation of *Illyrionethes* coastal species coincides with the Messinian salinity crisis (6–5.3 Myr ago). Several mainland clades of the *heroldi* lineage have also split during the same period. The prevailing hypothesis is that the Messinian salinity crisis is responsible for the invasion of the subterranean forms from marine habitats (e.g. Deharveng et al. 2019). Recent studies suggest that during that period a radiation within different subterranean Dinaric taxa occurred, both terrestrial and aquatic (Sbordoni et al. 1980; Zakšek et al. 2007; Delić et al. 2017a; Bilandžija et al. 2013; Njunjić et al. 2018), as it happened for other Mediterranean subterranean fauna (e.g., Faille et al. 2018). The Pleistocene species origin hypothesis (e.g., Vandel, 1964; Barr & Holsinger, 1985) was confirmed only by speciations within the *strasseri* lineage, while speciations within *heroldi*- and *magnus*-lineage occurred during Miocene or Pliocene. Similar timings were found in *Niphargus* species (Delić et al. 2017a).

The estimation of divergence times does not offer any idea about which type of habitats species have been occupying during different geological periods. Two main different possibilities could play a role in shaping the evolutionary history of *Illyrionethes* in the Dinaric Karst. The lineage diversifications could have occurred already in a surface ancestor, which subsequently colonized subterranean habitats multiple times independently. Those populations (present-day lineages) came into secondary contact since they were already reproductively isolated, and their evolution continued to occur independently. A similar situation was proposed for other Dinaric stygobionts (Zakšek et al. 2007). Another scenario is that it was a single colonisation of subterranean habitats, followed by multiple dispersal and speciation events, similar to the scenario proposed for the Dinaric troglobiotic genus *Anthroherpon* Reitter, 1889 (Coleoptera, Leiodidae) by Njunjić et al. (2018).

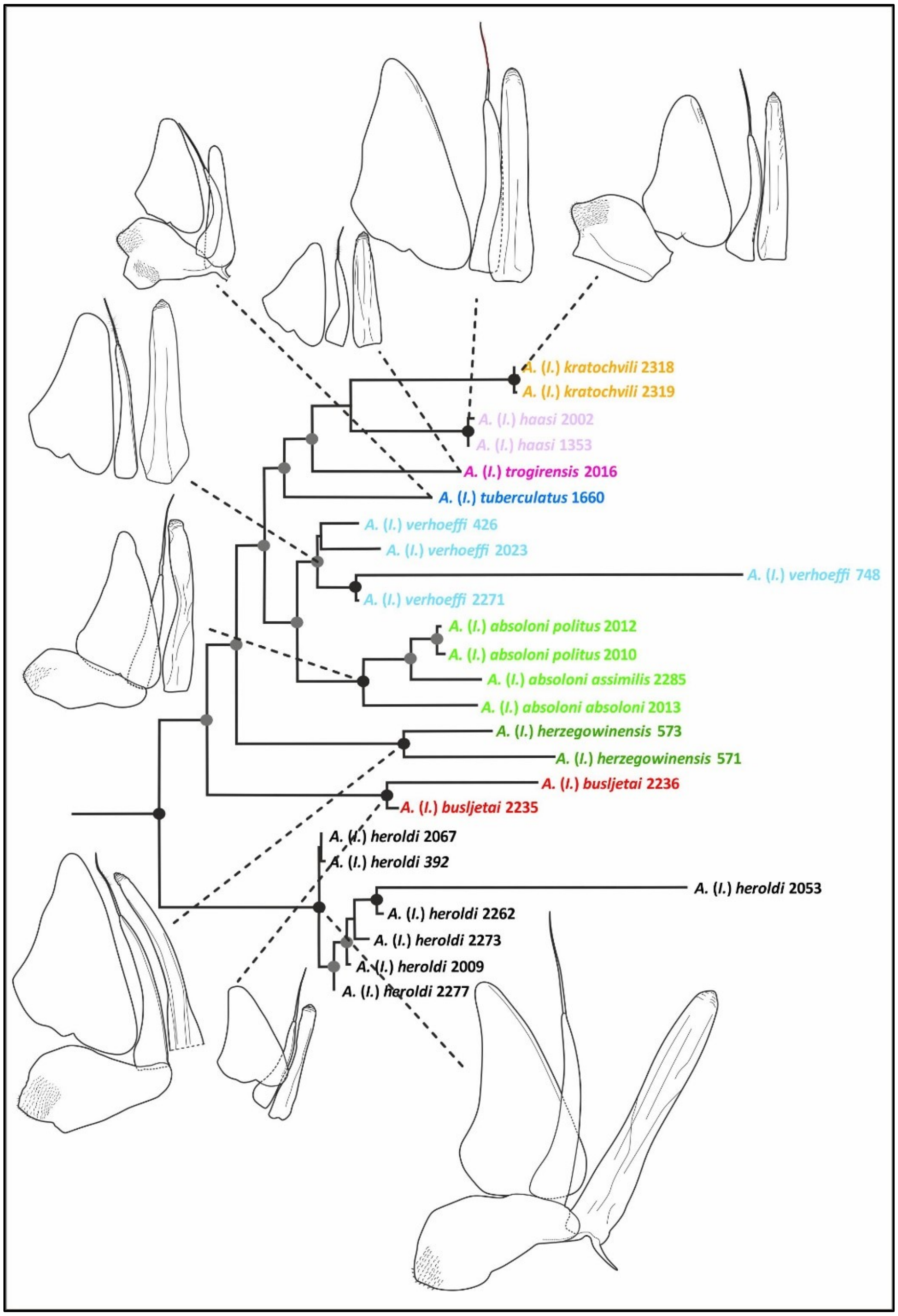

Figure 3. *Alpioniscus* (*Illyrionethes*), the *heroldi*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pleopod 1. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Partly adapted from Bedek et al. 2019a and 2019c, with permission.

Morphological analyses

The two morpho-groups previously suggested by Bedek & Taiti (2011), *heroldi*- and *strasseri*-morpho-group, correspond in part to the lineages identified by molecular analyses. The *heroldi*-morphogroup comprised *heroldi*- and *magnus*-lineage and the *strasseri*-morphogroup is consistent with the *strasseri*-lineage with the only difference of *A. absoloni* belonging to the *heroldi*-lineage instead of to the *strasseri*- lineage.

From a morphological point of view, the *strasseri* lineage can be distinguished from *heroldi* and *magnus* lineages by the deeply concave outer margin of the male pleopod 1 exopod in regards to no or slightly concave outer margin as proposed by Bedek & Taiti (2011). The other distinguishing character proposed by Bedek & Taiti (2011), the prominent hump on the male pereopod 7 carpus, is a common feature in the *strasseri* lineage but also present in *A. absoloni* and *A. magnus*. The morphological analyses did not reveal any character which could distinguish *magnus*- and *heroldi*-lineage, which is in agreement with the preliminary morphological analyses of Bedek & Taiti (2011).

Differential characters review:

Body length. The length of the body varies, in males from 3.5 mm (*A. mandalinae*) to 10.2 mm (*A. magnus*) and females from 5.3 mm (*A. lossinii*) to 11.2 (*A. magnus*) (Figure 8-Figure 10; Table C 1).

Body tegument. All Dinaric *Illyrionethes* species are unpigmented and without eyes. The majority of the species have smooth dorsum, all *strasseri*-lineage species, *A. magnus* and *A. drazinai* from the *magnus*-lineage, and *A. heroldi, A. haasi, A. kratochvili, A. herzegowinensis, A. verhoeffi* Neretva population and *A. busljetai* the *heroldi*-lineage. In some cases, there are posterior ridges on different somites, i.e. *A. balthasari* Cetina-Krka population, *A. drazinai, A. herzegowinensis, A. verhoeffi* Neretva population and *A. busljetai.* The species with granulated tegument always have ridges on posterior margins of some somites. The most granulated tergites are present in *A. tuberculatus*, whereas *A. absoloni*, *A. lossinii, A. trogirensis* and *A. mandalinae* are less granulated (Figure 8-Figure 10; Table C 1).

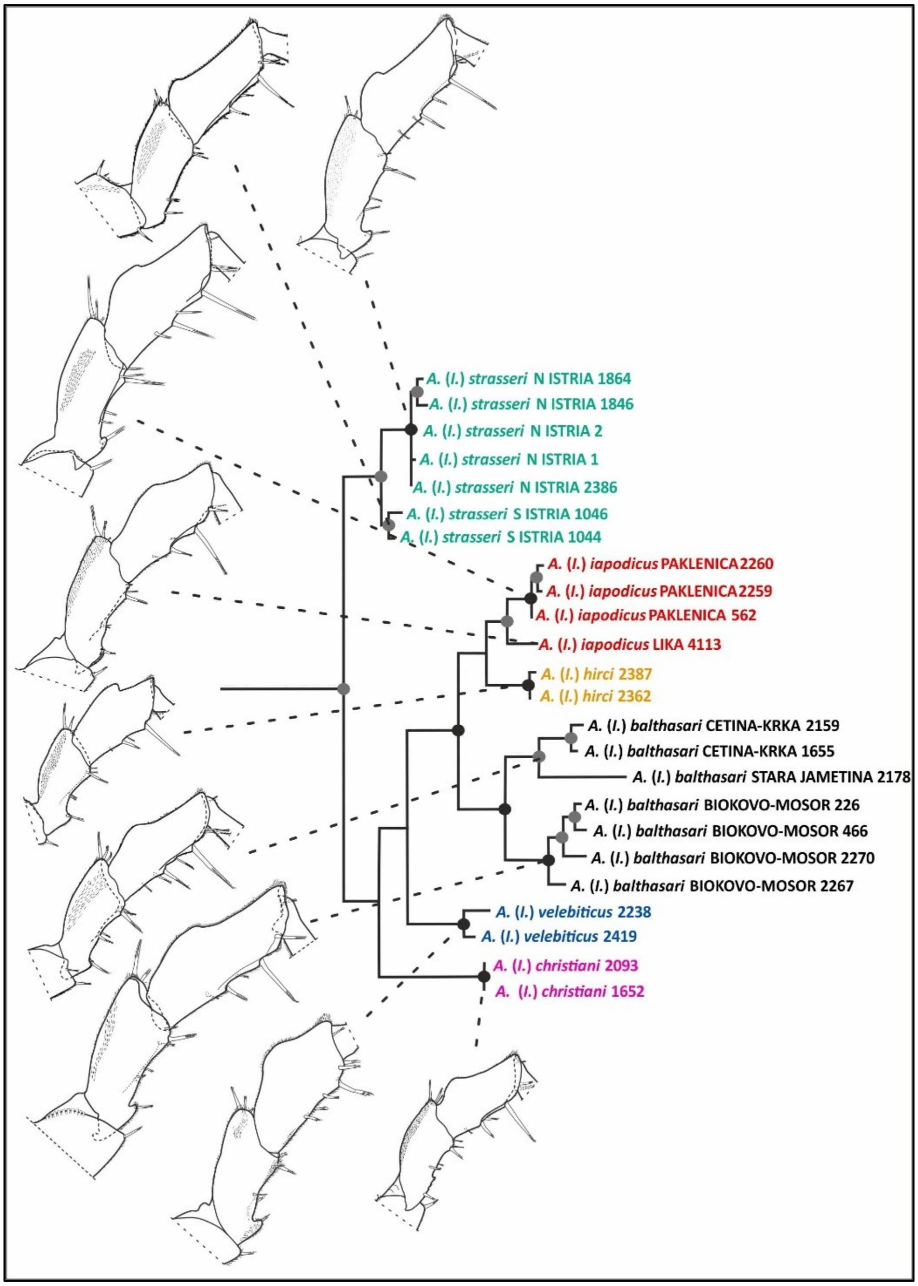

Figure 4. *Alpioniscus* (*Illyrionethes*), the *strasseri*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pereopod 7 carpus and merus. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Adapted from Bedek et al. 2017 and 2019c, with permission.

Antennulae. The difference of articles length–width relations were observed only between *A. velebiticus* and other *strasseri*–lineage species (Figure B 2, Table B 7). A number of aestetascs on the apical margin of the third article vary from three to seven (*A. velebiticus*) up to from seven to

14 (*A. balthasari* Biokovo-Mosor population), and statistically significant differences were observed only between a few species of *strasseri*–lineage (Table B 4, Table C 1).

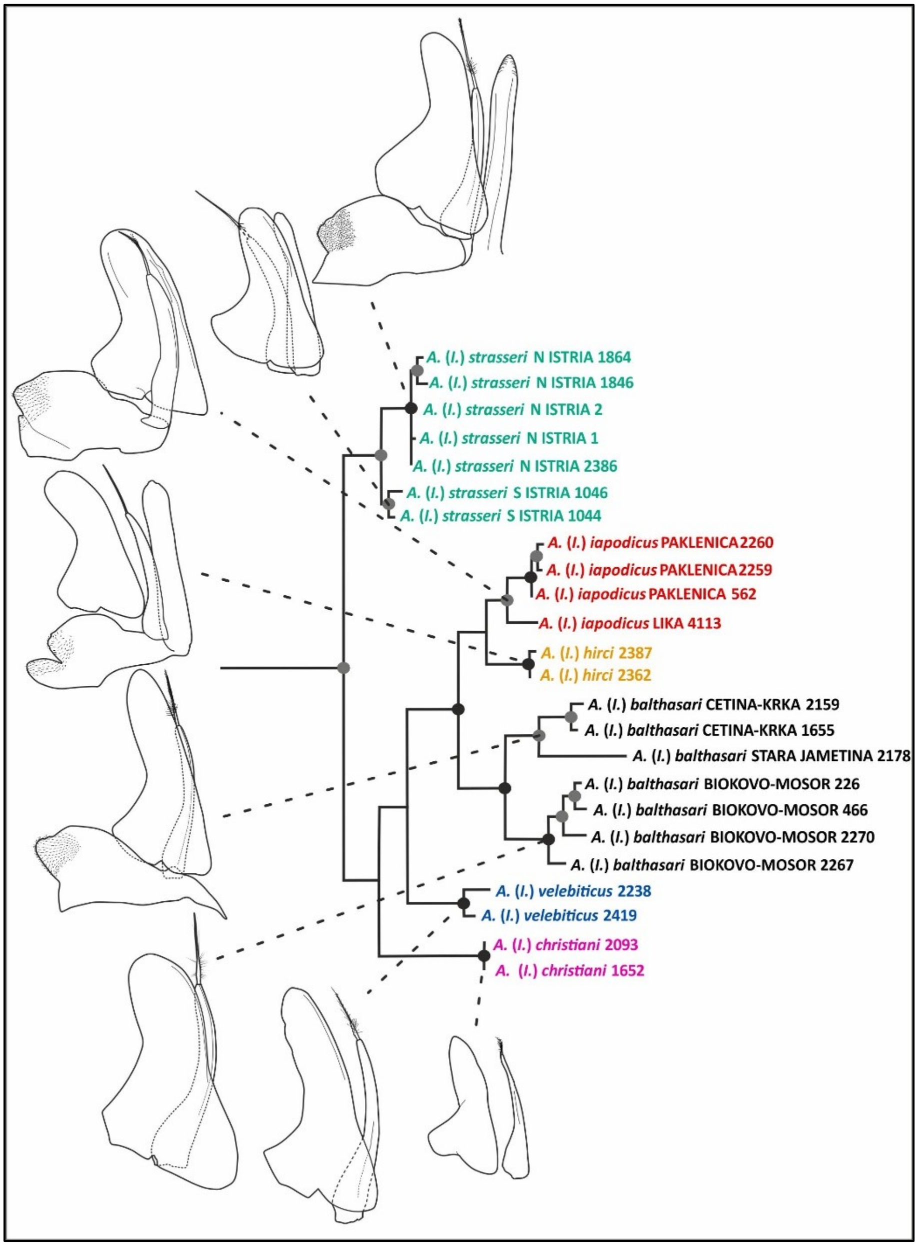

Figure 5. *Alpioniscus* (*Illyrionethes*), the *strasseri*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pleopod 1. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Adapted from Bedek et al. 2017 and 2019c, with permission.

Antennae. All the species of the *strasseri*-lineage as well as *A. magnus, A. heroldi, A. haasi,* and *A. kratochvili* have smooth peduncle, while all other species have more or less granulated peduncle. Interspecific variations of article relations (lengths and widths) do not show any significant differences among species. The differences were observed only between a few *strasseri*–lineage species (Table B 7). The numbers of flagellum articles vary from five to seven (*A. busljetai, A. trogirensis*, and *A. tubercualtus*) up to from eight to 13 (*A. balthasari* Cetina-Krka population), but the observed differences are statistically significant only between *A. velebiticus* and other *strasseri*–lineage species (Table B 4). The numbers of flagellum articles bearing aestetascs vary from two to three (*A. trogirensis*) up to from two to seven (*A. balthasari* Cetina-Krka population) (Table C 1), but the observed differences are statistically significant only between *A. balthasari* Cetina–Krka population and other *strasseri*–lineage species (Table B 4).

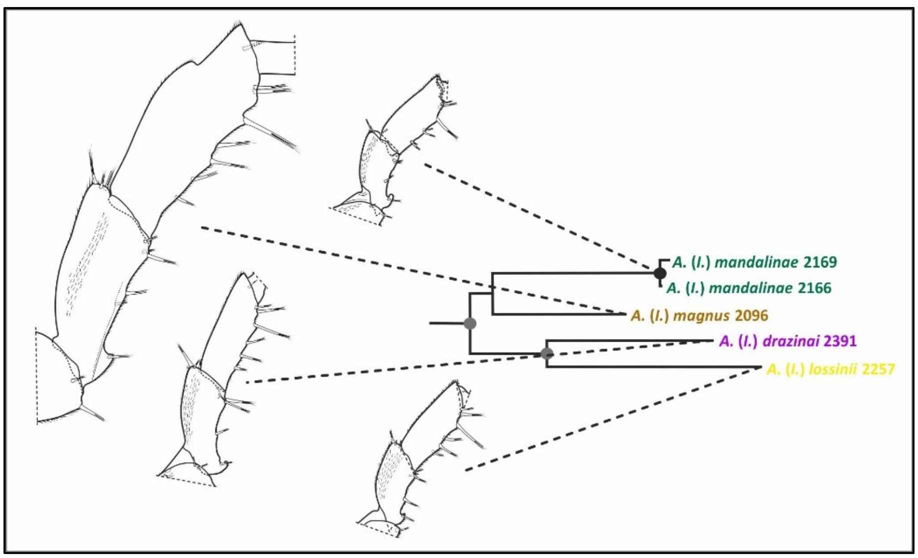

Figure 6. *Alpioniscus* (*Illyrionethes*), the *magnus*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pereopod 7 carpus and merus. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Adapted from Bedek et al. 2019b and 2019c, with permission.

Buccal pieces. Mandibles have one penicil in the right and three penicils in the left; while molar process has one penicil in the right and none in the left. The outer branch of maxillula has 5+6 apical teeth and two slender stalks. The inner branch has three penicils, with outer and middle penicils subequal, while the inner one is distinctly longer. The apex of the maxilla is setose and bilobate, with the inner lobe more or less wider than the outer one. The endite of the maxilliped is narrow, with a large and segmented apical penicil. The palp of the maxilliped distally has three rounded lobes, and the basal article has two small compound setae. The basis has a rounded outer lobe protruding posteriorly and is covered with long setae on the margin.

Male pereopod 1. The number of sternal setae on pereopod 1 carpus vary from four to five (*A. velebiticus, A. mandalinae, A. tuberculatus* and *A. absoloni*) to six to nine (*A. balthasari* Biokovo–Mosor population) (Table C 2), but the observed differences are statistically significant only between few *strasseri*–lineage species (Table B 4).

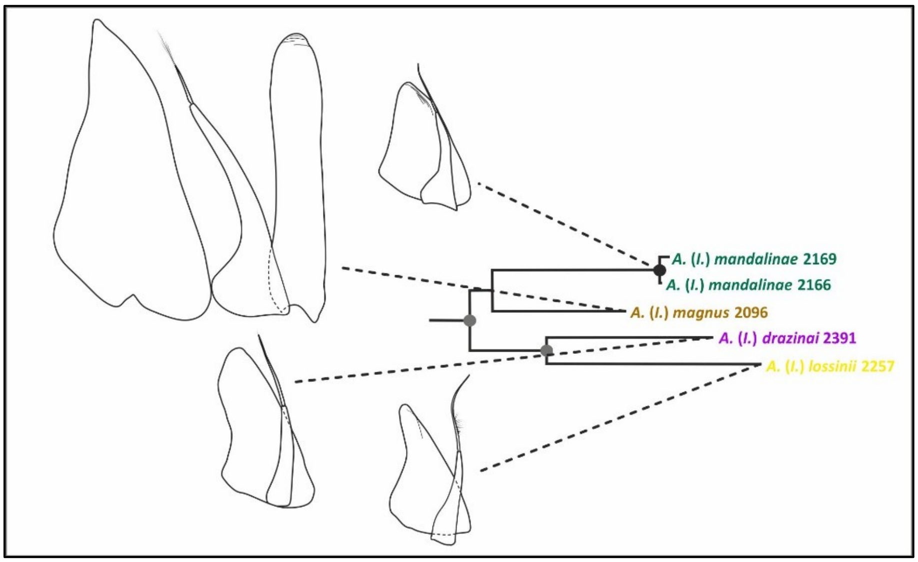

Figure 7. *Alpioniscus* (*Illyrionethes*), the *magnus*-lineage. Maximum likelihood (ML) phylogenetic tree obtained by 16S data set with male pleopod 1. Black and grey dots indicate bootstrap values of ≥0.95 and >0.75, respectively. Adapted from Bedek et al. 2019b and 2019c, with permission.

Male pereopod 7. The merus sternal lobe differs in its shape, it is in the form of a hook in the majority of species. The exceptions are *A. strasseri* S Istria population and *A. heroldi* with a hump without teeth, *A. christiani* with a hump with teeth and *A. herzegowinensis* with a double hump. The position and size of the lobe differ in different species (Figure 2, Figure 4, Figure 6, Figure B 3; Table C 2).

The carpus tergal hump is prominent in *A. strasseri, A. hirci*, *A. velebiticus*, *A. balthasari, A. iapodicus, A. christiani, A. magnus,* and *A. absoloni*. It differs in shape, position, length, and height (Figure 2, Figure 4, Figure 6; Table C 2). The hump ending and top positions significantly vary between majorities of *strasseri*–lineage species (Figure B 2, Table B 7). In *A. busljetai, A.*

trogirensis and *A. verhoeffi* Biokovo population, the tergal hump is present only in the largest specimens. The rest of the species lack the hump completely (Figure 2, Figure 4, Figure 6; Table C 2).

Figure 8. *Alpioniscus* (*Illyrionethes*), photos of *heroldi*-lineage species in situ. A, *A. kratochvili* topotype from Markova špilja, Hvar island; B, *A. haasi* topotype from Pišurka, Korčula island; C, *A. trogirensis* topotype from Špilja od Bilosoja, Trogir; D, *A. tuberculatus* topotype from Goranova pećina, Livno; E, *A. verhoeffi* from Kaverna pod vijaduktom kod Puljana, Neretva; F, *A. absoloni* from Novakuša pećina, Nevesinje; G, *A. herzegowinensis* from Pavlova pećina, Bihovo; H, *A. busljetai* topotype from Markova špilja, Seline; I, *A. heroldi* from Jama u Zagrebištu, Bileća. Scale bars: 1 mm. A, C-G, I, photo by J. Bedek; B, photo by H. Bilandžija; H, photo by P. Kutleša, adapted from Bedek et al. 2019a (used with permission).

Genital papilla. The shape of the genital papilla does not show any interspecific variations, only the ratio of width and tip width show interspecific variability between few *strasseri*–lineage species (*Figure B 2,*, Table B 7).

Male pleopod 1. The posterior apex of exopod differs in shape in the different species, from pointed (*A. christiani, A. magnus*) to broadly rounded (*A. hirci, A. iapodicus,* and *A. balthasari* Biokov-Mosor population). The width of the apex (measured as the ratio of exopod length and apex width) varies among different *strasseri*–lineage species (Figure B 2,, Table B 7). The outer margin of exopod can be almost straight (*A. mandalinae*), sinuous (*A. haasi, A. herzegowinensis, A. trogirensis, A. drazinai, A. magnus,* and *A. verhoeffi* Biokovo population), slightly concave (*A. heroldi, A. busljetai, A. absoloni, A. lossinii, A. verhoeffi* Neretva population, *A. kratochvili, A. tuberculatus*) to deeply concave (all *strasseri*-lineage species). The ratios of the length and concavity turning point position show interspecific variations among *strasseri*-lineage species (Table B 7). The endopod is usually narrow with almost parallel sides. The exceptions are *A. magnus* and *A. mandalinae* where the basal part of endopod is wide and outer margin is concave. The apical seta of the endopod is usually plumose, except with *A. hirci, A. heroldi, A. busljetai,* and *A. mandalinae.* (Figure 3, Figure 5, Figure 7, Table C 3) The ratio of lengths of exopod and endopod show interspecific variability between few *strasseri*–lineage species (Figure B 2,, Table B 7).

To conclude, species diagnostic characters with the highest specific discriminant values are: i) shape of the male pleopod 1 exopod outer margin; ii) the shape and position of the male pereopod 7 merus sternal lobe; iii) presence, length, and shape of the male pereopod 7 carpus tergal hump. Additional differential characters, informative only for a subset of species, are: i) the ratio of the length and concavity turning point position in the male pleopod 1 exopod; ii) the shape of posterior apex of the male pleopod 1 exopod; iii) the shape of the basis of the male pleopod 1 endopod; iv) body size; v) granulation of the tegument; vi) granulation of the antennal peduncle.

Population variabilities

Several species show intraspecific molecular divergence as well as small but consistent morphological differences between different populations. *Alpioniscus strasseri* includes two subclades, supported by molecular and morphological analyses (Figure 4, Figure 5, Figure B 2, Figure B 3, Table B 7, Table C 2, Table C 3). The distinct subclades correspond to different geological regions of the Istrian peninsula (northern and southern Istria). Moreover, the population from the island of Cres as well as the one from the surroundings of the town of Buzet in Istria, previously identified as *A. strasseri* (Verhoeff 1938; Bedek et al. 2011; Ozimec et al. 2011; Polak et al. 2012), show some differences.

The difference between populations of *A. iapodicus* is also supported by molecular and morphological analyses (Figure 4, Figure 5, Figure B 2, Figure B 3, Table B 7, Table C 2, Table C 3). They occur in Lika and Paklenica regions and are separated by the Velebit Mountain. The population which surrounds Velebit Mt. (in the Paklenica, the valley of Zrmanja river and foothills of Crnopac), previously identified as *A. balthasari* (Bedek et al. 2011) show some similarities but as well some differences with *A. iapodicus*.

Figure 9. *Alpioniscus* (*Illyrionethes*), photos of *strasseri*-lineage species in situ. A, *A. strasseri* from Grotta dei Partigiani, Trieste; B, *A. iapodicus* from Medina pećina, Perušić; C, *A. hirci*, topotype from Bukovac, Fužine; D, *A. balthasari* topotype from Kotluša, Cetina; E, *A. velebiticus* from Lukina jama – Trojama, Velebit; F, *A. christiani* topotype from Biserujka, Krk island. Scale bars: 1 mm. A, B, D-F, photo by J. Bedek; C, photo by M. Lukić (used with permission), B, adapted from Bedek et al. 2017 (used with permission).

Alpioniscus balthasari comprises three subclades (Cetina-Krka, Stara jametina and Biokovo-Mosor), clearly seen in 16S BI tree and supported by morphological analyses (Figure 4, Figure 5, Figure B 2, Table B 7, Table C 2, Table C 3). Even though the morphological differences and 16S distance borderline are consistent with the species level, the population in between has to be analyzed in more detail to solve their relationships. Moreover, the populations from the Dinara Mt. (Strouhal 1939c; Bedek et al. 2011), Tomislavgrad (Buturović 1955b), Stolac (Horvatović 2014), should be analysed in the future, same as those from surroundings of Velebit Mt., as previously mentioned.

The molecular analyses grouped the *A. verhoeffi* specimens, but with high interpopulation COI/16S distances (up to 19/31%). The differences are supported by morphological analyses (Table C 1, **Table C 3**), but more specimens should be analyzed in more detail to solve their relationships.

The differences of *A. absoloni* subspecies described by Strouhal (1939a) were not confirmed by morphological analyses, even though they were clearly separated by molecular analyses. More material should be analysed, both morphologically and molecularly, to resolve the status of these subspecies.

Overall, these results suggest an ongoing speciation process, perhaps as a consequence of recent geographical isolation.

Figure 10. *Alpioniscus* (*Illyrionethes*), photos of *magnus*-lineage species in situ. A, *A. mandalinae* topotype from Mandalina, Šibenik; B, *A. magnus* topotype from Bazgovača, Brač island; C, *A. drazinai* topotype from Strašna peć, Dugi otok island; D, *A. lossinii* topotype from Medvjeđa špilja, Veli Lošinj island. Scale bars: 1 mm. Photo by J. Bedek.

Biogeographical observations

The three lineages identified in this study, *strasseri-, heroldi-* and *magnus*-lineage, follow a northwest-southeast direction, the so-called *Dinaric direction* (Zupan Hajna, 2012). They have overlapping distributions, where the *strasseri*-lineage is the most widely distributed, from Italy in the NW of the Dinaric Karst to the south of Biokovo Mt., the *heroldi* lineage occurs from north Dalmatia in the NW to the SE Herzegovina, while the provisional *magnus* lineage occupies the coast from the island of Lošinj to the island of Brač.

Although the sympatry within the Dinaric *Illyrionethes* is not uncommon, the syntopy is relatively rare. *Alpioniscus heroldi* is syntopic with *A. absoloni* in the area of Bileća, with *A. verhoeffi* in the area of the river Neretva and the Biokovo Mt., and with *A. balthasari* on the Biokovo Mt. The three *Illyrionethes* lineages have overlapping ranges even though syntopic species are relatively rare. The syntopic species came into contact since they were already reproductively isolated. The rareness of syntopy is probably due to ecological (e.g., competition) rather than geographical reasons. All species in the *strasseri* lineage are not syntopic and always occur in geographically or altitudinally separated areas (e.g., *A. velebiticus* Bedek & Taiti on the higher elevation of Velebit Mt. compared to *A. iapodicus*).

Unlike other troglobionts in the Dinaric Karst which are usually restricted to smaller geographical units, several *Alpioniscus* species show large ranges. The amphibian species show large ranges according to our study (*A. balthasari* ca. 130 x 50 km, *A. heroldi* ca 125 x 35 km, *A. strasseri* ca. 120 x 80 km, *A. velebiticus* ca. 110 x 10 km), likely because they can use both aquatic and terrestrial dispersal pathways. The large range is shown also by *A. iapodicus* (ca 75 x 35 km), which do not apparently have an amphibian way of life. Five species are known from a single or just two caves, i.e. *A. christiani, A. lossinii, A. busljetai, A. mandalinae,* and *A. tuberculatus*. Six more species are restricted to a relatively small area (≤175 km^2): *A. magnus, A. drazinai, A. trogirensis, A. herzegowinensis, A. haasi,* and *A. kratochvili*. From these, nine species are restricted to the coastal area (all except *A. tuberculatus* and *A. herzegowinensis*), but the range of four of occur on both mainland coast and islands, or different islands: *A. christiani* (Krk Island and mainland)*, A. drazinai* (Dugi otok Island and Kornati archipelago)*, A. trogirensis* (Čiovo and Šolta Islands)*,* and *A. haasi* (Korčula Island and Pelješac Penninsula).

A very peculiar distribution pattern, the paralittoral one, is present in the tentative *magnus*-lineage. Such a distribution was never previously reported for troglobionts and is usually exhibited by anchialine species, such as *Hadzia fragilis* S. Karaman, 1932, *Niphargus hebereri* Schellenberg, 1933 (Amphipoda), *Tethysbaena halophila* (S. Karaman, 1953) (Thermosbaenacea) (Sket, 2005), and by the stygobiont *Sphaeromides virei virei* (Brian, 1923) (Isopoda, Cirolanidae) (Sket 2012).

CONCLUSIONS

1. Altogether 12 out of 13 nominal species are confirmed. The existence of the three nominal subspecies was inconclusive within the study. The nominal species, *A. bosniensis* is considered to be a junior synonym of *A. heroldi*.
2. Seven out of 12 putative undescribed species are confirmed (the remaining five species were not analysed within this study). All confirmed new species are described: *A. iapodicus* Bedek, Horvatović and Karaman, 2017, *A. hirci* Bedek & Taiti, 2019, *A. velebiticus* Bedek & Taiti, 2019, *A. lossinii* Bedek, Gottstein and Taiti, 2019, *A. drazinai* Bedek, Gottstein and Taiti, 2019, *A. mandalinae* Bedek, Gottstein and Taiti, 2019 and *A. busljetai* Bedek, Gottstein and Taiti, 2019.
3. At the moment Dinaric *Illyrionethes* includes 19 nominal and five putative undescribed species. Altogether 32 nominal troglobiotic species within the family Trichoniscidae are present (from genera *Alpioniscus, Aegonethes, Titanethes, Cyphonethes, Protonethes, Cetinjella, Andronicus, Strouhaloniscellus, Cyphoniscellus, Thaumatoniscellus*) in the Dinaric Karst.
4. The Dinaric *Illyrionethes* species are grouped in three lineages: *heroldi*-, *strasseri*- and tentative *magnus*-lineage. Nine species are comprised in the *heroldi*-lineage: *A. heroldi, A. haasi, A. kratochvili, A. absoloni, A. trogirensis*, *A. verhoeffi*, *A. tuberculatus, A. herzegowinensis,* and *A. busljetai*. The *strasseri*-lineage comprises six species: *A. strasseri; A. balthasari, A. christiani, A. hirci,* and *A. velebiticus*. The *magnus*-lineage includes four species: *A. magnus, A. lossinii, A. drazinai,* and *A. mandalinae*.
5. The three lineages of Dinaric *Illyrionethes* split ~10-9 Myr ago, while speciations occurred from ~10 to 2 Myr ago.
6. Even small morphological differences among different species are reliable diagnostic characters.
7. The *strasseri*-lineage can be distinguished from *heroldi*- and *magnus*-lineages by the deeply concave outer margin of the male pleopod 1 exopod in regards to no or slightly concave outer margin. The morphological analyses did not reveal any character which could distinguish *magnus*- and *heroldi*-lineage.

8. Species diagnostic characters with the highest specific discriminant values are: i) the shape of the male pleopod 1 exopod outer margin; ii) the shape and position of the male pereopod 7 merus sternal lobe; iii) presence, length, and shape of the male pereopod 7 carpus tergal hump.
9. The three lineages follow a northwest-southeast direction, with overlapping distributions.

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APPENDICES

Appendix A. Taxonomy of the *Alpioniscus* (*Illyrionethes*), *heroldi*-lineage species

Specimens were hand collected with tweezers, fixed and stored in 75% ethanol with glycerol or 96% ethanol. Several specimens were dissected and mounted for micropreparations in Hoyer's medium (Anderson 1954). For identifications and illustrations in the description, the entire body and the following appendages were used: antennae, antennulae, buccal pieces, male pereopods 1 and 7, genital papilla and male pleopods 1 and 2. Specimens were examined under a Zeiss Stemi 2000-C, Zeiss Primo Star and Nikon Labophot microscopes. Micropreparations were photographed using Canon EOS 40D and EOS Utility software. Drawings were made from photographs using CorelDRAW X8. The examined material, description, etymology and remarks are given. The following numerical characters were counted: the number of (1) antennular aesthetascs, (2) antennal flagellum articles, (3) antennal flagellum articles bearing aesthetascs, and (4) setae on the male pereopod 1 carpus. The terminology used in species description is mainly based on Vandel (1960; 1962). The locality coordinates used the WGS84 datum. The map was drawn using ArcMap 10.1 software and related Shadow Relief layer.

Abbreviations:

CBSSC	Croatian Biospeleological Society Collection, Zagreb, Croatia
CNHM	Croatian Natural History Museum, Crustacea Collection, Zagreb, Croatia
MZUF	Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia La Specola, Florence, Italy
SMNS	Staatliches Museum für Naturkunde Stuttgart, Isopod Collection, Stuttgart, Germany
ZCDB	Zoological Collection at the Department of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

TAXONOMY

Family Trichoniscidae Sars, 1899

Subfamily Trichoniscinae Sars, 1899

Genus *Alpioniscus* Racovitza, 1908

Subgenus *Illyrionethes* Verhoeff, 1927

Alpioniscus* (*Illyrionethes*) *heroldi (Verhoeff, 1931)

Figure A.1–Figure A. 4, Figure A. 19

Illyrionethes heroldii Verhoeff 1931a: 22, figs 4–6.–Frankenberger 1937: 173.–1938: 25-28, 30, 34, fig. II.

Illyrionethes heroldi.–Strouhal 1938: 274-275, figs 9–11.–1939a: 7–16.–1939b: 117, 122–125, map [partim: *nec* Lok. 806, "Čelina Jama"; hoch über dem Popovo Polje in Richtung Grepci gelegen].–1939c: 18, 23, 25, 28, 29 [partim: *nec* Čelina jama (Lok. 809), hoch über dem Popovo polje in Richtung Grepci, S. Herzegowina].–1940: 89, 95.–Frankenberger and Strouhal 1940: 448, 449, plate 6.–Buturović 1951: 97–105.

Illyrionethes bosniensis.–Frankenberger 1939: 99–101, figs 1–3.–Frankenberger and Strouhal 1940: 448, 450, plate 6.–Strouhal 1940: 95.

Alpioniscus heroldi.–Legrand 1946: 255.–Vandel 1947: 271.–Potočnik 1989: 64.–Erhard 1996: 3.–Schmalfuss 2003: 13.–Bedek et al. 2011: 238, 270, 316, fig. 13.–Hlaváč et al. 2019: 99.

Alpioniscus (*Illyrionethes*) *heroldi*.–Vandel 1946: 160.–Buturović 1957: 6, 9, 14, 22, 34, 49, figs 6, 8, 24.–Schmölzer 1965: 60, figs 227, 228.–Karaman 1966: 377.–Sket 1986: 484.–Potočnik 1993: 84, 85 178.–Tabacaru 1996: 35.–Sket 2003: 184.–Horvatović 2014: 125, 176, 177, 223, 240, fig. 7.28.–Karaman and Horvatović 2018: 266.–Bedek et al. 2019b: 491.–2019c: fig 5.

Alpioniscus (*Illyrionethes*) *bosniensis*.–Buturović 1955: 133, 134, fig. 5.–1957: 9, 14, 34, 37, 49, fig. 24.–Schmölzer 1965: 61, figs 229, 230.–Karaman 1966: 377.–Sket 1986: 484.–Potočnik 1993: 84, 178.–Tabacaru 1996: 36.–Horvatović 2014: 126, 177, 240, fig. 7.28.–Bedek et al. 2019c.

Alpioniscus bosniensis.–Potočnik 1989: 64.–Schmalfuss 2003: 13.–Bedek et al. 2011: 238, 267, fig. 10.

Alpioniscus sp.–Giachino et al. 2011: 370 [partim: Majića ponor].

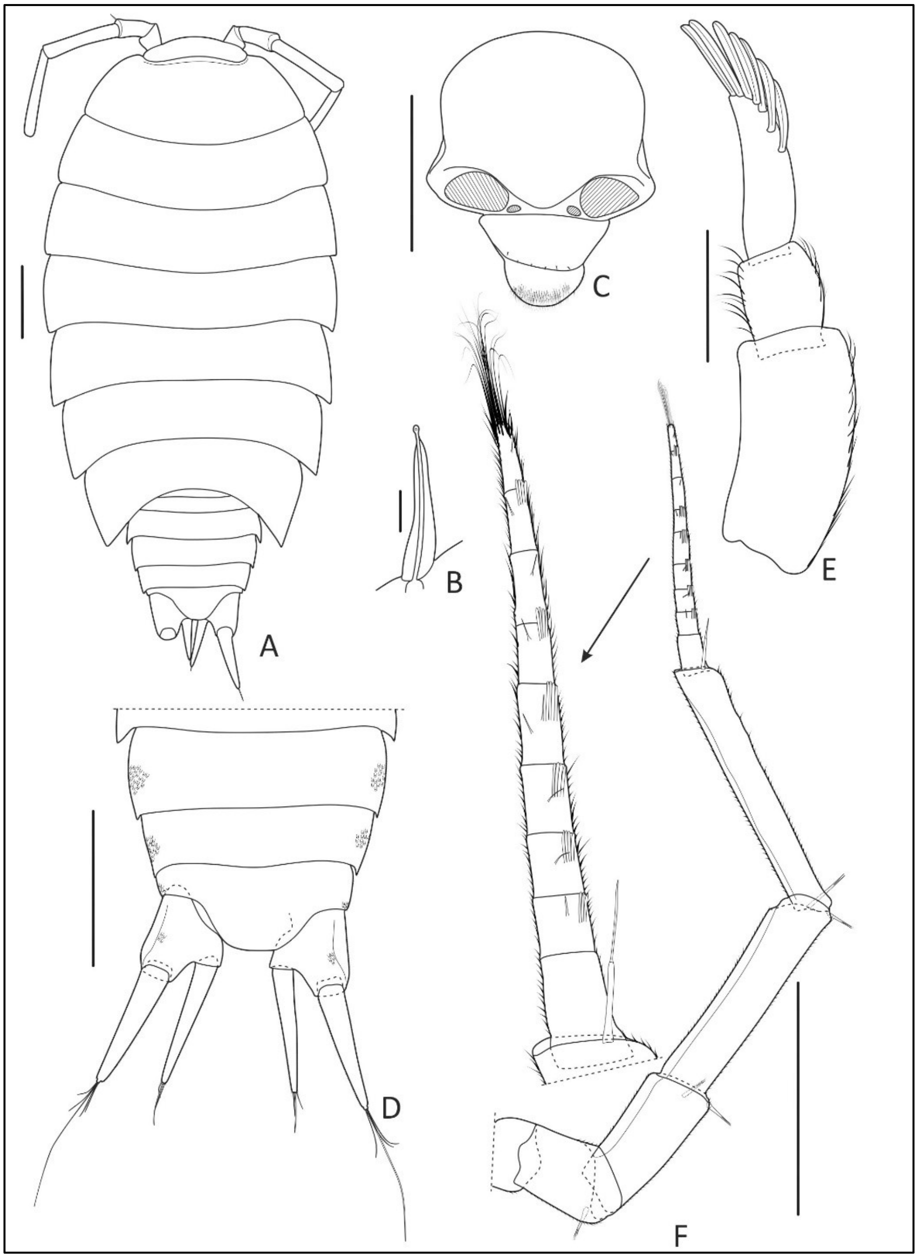


Figure A.1. *Alpioniscus* (*Illyrionethes*) *heroldi* ♂ CBSSC IT2427 from Jama u Zagrebištu. **A** habitus in dorsal view; **B** dorsal scale-seta; **C** cephalon, dorsal; **D** pleonites 4, 5, telson and uropods; **E** antennula; **F** antenna with enlargement of flagellum. Scale bars: 1 mm (**A, F**), 0.1 mm (**C–E**), 0.01 mm (**B**).

Material examined. BOSNIA AND HERZEGOVINA. **Herzegovina, Bileća**: 2 ♂♂, Granica, Jama u Zagrebištu (cave), 42.9198°N, 18.3491°E, 14.IX.2006, S. Ognjenović leg., CBSSC IT2277; 3 ♂♂, same locality, 4.IX.2011, J. Bedek leg., CBSSC IT2427; 3 ♂♂, 2 ♀♀, same data, CBSSC

IT2432; 2 ♂♂, same locality and date, CBSSC IT2430; **Herzegovina, Bijeljani**: 1 ♂, Dabarasko polje, Ljelješnica (cave), 43.0479°N, 18.2628°E, 8.VIII.2005, P. Trontelj, S. Polak leg., CBSSC IT3198; 2 ♂♂, 1 ♀, same data, ZCDB; **Herzegovina, Fatnica**: 5 ♂♂, 5 ♀♀, Fatničko polje, Obodska pećina (cave), 43.0181°N, 18.3482°E, VII.1987, CBSSC IT2887; 29 ♂♂, 50 ♀♀, 3 juvs, same data, ZCDB; 2 ♀♀, same locality, 8.VIII.2005, P. Trontelj, S. Polak leg., CBSSC IT3199; 1 ♂, 4 ♀♀, same data, ZCDB; **Herzegovina, Trebinje**: 1 ♂, Grebca, Ravno, Debeljin (cave), 43.6422°N, 17.2302°E, 13.VIII.2005, S. Polak, P. Trontelj, leg., CBSSC IT3634; 1 ♂, 2 ♀♀, same data, ZCDB; 1 ♂, Grebca, Ravno, Grabovica (cave), 42.7437°N, 18.0577°E, 13.VIII.2005, P. Trontelj, S. Polak, leg., ZCDB; 1 ♂, 3 ♀♀, Popovo polje, Zavala, Vjetrenica (cave), 42.8460°N, 17.9838°E, 6.IX.2001, B. Jalžić, leg., CNHM 4/1610; 1 ♂, same locality, VIII.2004, CBSSC IT2051; 1 ♂, 1 juv., same locality, 16.VIII.2004, M. Pavlek leg., CBSSC IT2048; 1 ♀, same locality and date, R. Ozimec leg., CBSSC IT2070; 1 ♂, 1 ♀, 1 juv., same locality and date, H. Bilandžija leg., CBSSC IT2073; 4 ♂♂, 4 ♀♀, 1 juv., same locality, 17.VIII.2004, M. Lukić leg., CBSSC IT2045; 1 ♀, same locality and date, M. Pavlek leg., CBSSC IT2068; 1 ♀, same locality and date, H. Bilandžija leg., CBSSC IT2074; 1 ♀, same locality and date, R. Ozimec leg., CBSSC IT2078; 3 ♂♂, 1 ♀, same locality, 18.VIII.2004, M. Pavlek leg., CBSSC IT2047; 1 ♀, same locality and date, R. Ozimec leg., CBSSC IT2054; 1 ♂, 1 juv., same locality and date, M. Pavlek leg., CBSSC IT2057; 1 ♂, 2 ♀♀, same locality and date, J. Bedek leg., CBSSC IT2067; 2 ♀♀, same locality and date, D. Basara leg., CBSSC IT2069; 1 ♀, same locality, 19.VIII.2004, J. Bedek leg., CBSSC IT2055; 3 ♀♀, same locality and date, H. Bilandžija leg., CBSSC IT2071; 1 juv. same locality and date, M. Lukić leg., CBSSC IT2079; 2 ♂♂, same locality, 20.VIII.2004, M. Lukić, J. Bedek leg., CBSSC IT2058; 1 ♂, 3 ♀♀, 1 juv., same data, CBSSC IT2075; 1 ♂, 4 ♀♀, 1 juv., same data, CBSSC IT2081; 1 ♂, same locality, 19.VIII.2005, J. Bedek leg., CBSSC IT389; 1 ♀, same locality, 22.VIII.2006, J. Bedek leg., CBSSC IT2052; 3 ♀♀, same locality, 20.VIII.2007, J. Bedek leg., CBSSC IT2053; 1 ♂, 1 ♀, same locality, 22.VIII.2007, J. Bedek leg., CBSSC IT2065; 1 juv., same locality and date, R. Ozimec leg., CBSSC IT2076; 2 ♂♂, same locality, 22.IX.2007, V. Zakšek leg., ZCDB; 3 ♂♂, 1 ♀, Popovo polje, Zavala, Bjelušica (cave), 42.8454°N, 17.9778°E, 17.VIII.2005, M. Lukić leg., CBSSC IT392; 1 ♂, 1 ♀, same locality and date, J. Bedek leg., CBSSC IT393; 1 ♂, 2 ♀♀, 1 juv., Popovo polje, Zavala, Gladulja (cave), 42.8469°N, 17.9938°E, 17.VIII.2005, J. Bedek leg., CBSSC IT386; 1 ♂, 5 ♀♀, same locality and date, M. Lukić leg., CBSSC IT388; **Herzegovina, Tomislavgrad**: 1 ♀, Donji Brišnik, Pećina u Donjem Brišniku (cave), 43.6422°N, 17.2302°E, 26.I.2007, J. Bedek, leg., CBSSC IT2008; 1 ♂, 1 ♀, same data, CBSSC IT2009; 1 ♀, Donji Brišnik, Grabovica, Listvača, 43.6399°N, 17.1933°E, 5.IX.2009, R. Ozimec leg., CBSSC IT2273; 3 ♂♂, same data, CBSSC IT2276; 1 ♂, Donji Brišnik, Grabovica, Jama kod Drmića staja, 9.IX.2010, R. Ozimec leg., CBSSC IT2274; 5 ♂♂, 1 ♀, Omerovići, Dahna (cave), 43.6565°N, 17.2089°E, 3.IX.2009, R. Ozimec leg., CBSSC IT2275; 2 ♂♂, same locality, 29.III.2012, A. Komerički leg., CBSSC IT3662; 3 ♂♂, 3 ♀♀, same locality and date, J. Bedek leg., CBSSC IT3663; 1 ♂, 1 juv., same locality and date, R. Ozimec leg., CBSSC IT3664; 1 ♀, same locality and date, T. Čuković leg., CBSSC IT3665; 2 ♀♀, same locality and date, M. Lukić leg., CBSSC IT3666; 1 juv., same locality and date, I. Napotnik leg., CBSSC IT3667; 4 ♀♀, Bukovica, Mala Bukovička špilja (cave), 28.III.2012., J. Bedek leg., CBSSC IT3668; 1 ♂, 2 ♀♀, 2 juvs, same locality and date, I. Napotnik, M. Vasić leg., CBSSC IT3669; 5 ♂♂, 1 ♀, same locality and date, A. Ćukušić leg., CBSSC IT3670; 8 ♂♂, 2 ♀♀, same locality and date, A. Komerički leg., CBSSC IT3671; 1 ♂, 2 ♀♀, same locality and date, T. Čuković leg., CBSSC IT3672; 1 ♂, 2. špilja u kamenolomu Čedari (cave), 11.IV.2009, M. Šumanović leg., CBSSC IT3675.

CROATIA. **Dalmatia, Dubrovnik**: 4 ♂♂, 2 ♀♀, 2 juvs, Osojnik, Jama u Zabirađu (cave), 42.7327°N, 18.0493°E, 30.III.2008., J. Bedek leg., CBSSC IT1294; 2 ♂♂, 2 ♀♀, same locality, 2.XI.2008, J. Bedek leg., CBSSC IT1296; 2 ♂♂, 3 ♀♀, Gromača, Špilja za Gromačkom vlakom (cave), 42.7435°N, 18.0274°E, 29.III.2003., J. Bedek leg., CBSSC IT2713; 2 ♂♂, 4 ♀♀, 2 juvs, Riđica, Zadubravica (cave), 42.7717°N, 17.9364°E, 31.III.2008., R. Ozimec leg., CBSSC IT1311; 3 ♂♂, 3 ♀♀, 2 juvs, same locality, 3.XI.2008, J. Bedek leg., CBSSC IT1313; 5 ♂♂, 1 ♀, same locality and date, M. Lukićleg., CBSSC IT1315; 3 ♂♂, 1 ♀, 1 juv., Trsteno, Brsečine, Kukova peć (cave), 42.7270°N, 17.9657°E, 7., 8.X.2009., R. Ozimec leg., CBSSC IT1680; 1 ♂, Ograđenica, Gumanci, Vilinska špilja (cave), 42.7979°N, 17.9227°E, 7., 4.XI.2008, R. Ozimec leg., CBSSC IT1349; 1 ♂, 1 ♀, same locality, 23.VI.2009., A. Komerički, K. Miculinić leg., CBSSC IT1690; 1 ♂, Točionik, Golubinka pod Grabovom grudom (cave), 16.X.2011, D. Basara leg., CBSSC IT2578; **Dalmatia, Pelješac**: 2 ♂♂, 1 ♀, Ston, Ponikve, Crno jezero (cave), 42.8473°N, 17.6365°E, 14.IV.2011, I. Njunjić leg., CBSSC IT2578; 1 ♂, same locality and date, R. Ozimec leg., CBSSC IT2564; **Dalmatia, Neretva**: 2 ♂♂, 4 ♀♀, Metković, Dobranje, Kolorepići, Ciganuša (cave), 10.I.1998, B. Jalžić leg., CBSSC IT3048; 2 ♂♂, 4 ♀♀, Metković, Dobranje, Kornjatuša (cave), 42.9791°N, 17.6740°E, 19.VII.1997, B. Jalžić leg., CNHM 6/1672; 4 ♀♀, Metković, Bebići, Golovrh, Maica golubinka (cave), 43.1089°N, 17.5664°E, 21.VI.2010, J. Bedek leg., CBSSC IT4111; 1 ♀, same data, CBSSC IT4494; 4 ♂♂, 1 ♀, Dragovija–Vid, Pavličevica (cave), 43.1061°N, 17.5874°E, 21.VIII.1997, B. Jalžić, CBSSC IT1158; 1 ♂, 1 ♀, same data, CNHM 2/1673; 2 ♂♂, 1 ♀, Ploče, Peračko blato, Pukotina u tunelu polje Jezero-Peračko blato (cave in tunnel), 43.0922°N, 17.4510°E, 24.VI.2010, A. Kirin leg., CBSSC IT2019; 4 ♂♂, 2 ♀♀, same locality and date, J. Bedek leg., CBSSC IT2020; 1 ♂, 1 ♀, 1 juv., same locality, 25.VIII.2005, M. Pavlek leg., CBSSC IT3008; 3 ♂♂, 1 ♀, Raba, Špilja na Zalokavlju (cave), 42.9682°N, 17.5271°E, 17.VII.1997, B. Jalžić leg., CNHM 4/1674; 3 ♂♂, 4 ♀♀, Opuzen, Dukati, Vištićina jama (cave), 42.9853°N, 17.5574°E, 16.VII.1997, B. Jalžić leg., CNHM 7/1675; 1 ♂, 1 ♀, same locality, 8.II.1998, S. Vujčić-Karlo leg., CBSSC IT2090; 2 ♂♂, same locality, 19.I.2002, V. Jalžić leg., CBSSC IT3056; **Dalmatia, Vrgorac**: 3 ♂♂, 1 ♀, 2 juvs, Dusina, Tunel Podprolog–Dusina (tunnel), 43.1900°N, 17.4267°E, 4.VIII.2009, H. Bilandžija leg., CBSSC IT3062; 3 ♂♂, 1 ♀, 2 juvs, same locality and date, B. Jalžić leg., CBSSC IT3103; 1 ♂, 2 ♀♀, 2 juvs, Majići, Ravča, Jasena ponor (cave), 43.2212°N, 172767°E, 13.VIII.2009, B. Jalžić leg., CBSSC IT2801; 10 ♂♂, 5 ♀♀, same locality, 4.VIII.2010, A. Kirin leg., CBSSC IT3058; 1 ♀, 2 juvs, same locality, 4.IX.2015, B. Jalžić leg., CBSSC IT4072; 4 juvs, same data, CBSSC IT4073; 1 ♂, Zavojane, Buklijaši, Ošlja jama (cave), 43.2504°N, 17.2869°E, 6.X.2018, N. Kuharić leg., CBSSC IT4295; 2 ♂♂, 7 ♀♀, 1 juv., same locality and date, V. Sudar leg., CBSSC IT4296; 2 ♂♂, 5 ♀♀, 1 juv., Mali Šibenik, Kozica, Antunovići, Jama na vrhu Malog Šibenika (cave), 43.2811°N, 17.2335°E, 19.VI.2011, B. Jalžić leg., CBSSC IT3080; 3 ♂♂, 7 ♀♀, 1 juv., same locality, 1.V.2012, T. Čuković leg., CBSSC IT4071; 1 ♂, same locality and date, R. Cvitanić leg., CBSSC IT4082; 9 ♂♂, Kozica, Antunovići, Mala špilja kod Antunovića (cave), 43.2770°N, 17.2270°E, 5.XII.2009, B. Jalžić, P. Bregović leg., CBSSC IT3151; 8 ♂♂, 8 ♀♀, same locality, 22.I.2016, M. Lukić leg., CBSSC IT3822; 1 ♂♂, ♀♀, Kozica, Antunovići, Velika špilja kod Antunovića (cave), 43.2768°N, 17.2273°E, 23.III.2004, R. Ozimec leg., CBSSC IT211; 1 ♂, 1 ♀, same locality, 13.XI.2010, H. Cvitanović leg., CBSSC IT2312; 1 ♂, 1 ♀, 3 juvs, same locality, 29.XI.2009, P. Bregović leg., CBSSC IT3150; 12 ♂♂, 7 ♀♀, same locality, 22.I.2016, M. Lukić leg., CBSSC IT3820; **Dalmatia, Biokovo Mt.**: 2 ♂♂, 1 ♀, Podgora, Šošići, Štedovac, Baba (cave), 43.2565°N, 17.1623°E, 27.IV.2002, B. Jalžić leg., CNHM 3/1681; 2 ♂♂, 3 ♀♀, 1 juv., same locality and date, R. Ozimec leg., CBSSC IT834; 1 ♂, 1 ♀, same locality, 16.X.2002, R. Ozimec leg., CBSSC IT837; 5 ♂♂, 1 ♀, 6 juv., same locality, 5.XI.2009, H. Cvitanović leg., CBSSC IT2262; 2 ♂♂, 2 ♀♀, 6 juv., same locality and date, R. Ozimec leg., CBSSC IT2263; 2 ♂♂, same locality, 17.XI.2011, D. Basara leg., CBSSC IT2541; 1 ♂, 2 ♀♀, Podgora, Šošići, Saranač, Jama pod Osojem (cave), 43.2514°N, 17.1184°E, 22.VI.2003, J. Bedek leg., CBSSC IT908; 1 ♂, same locality and date, G. Mišćenić leg., CBSSC IT952; 7 ♂♂, 5 ♀♀, Podgora, Vrata Biokova, Supin, Jama za Supinom (cave), 43.2504°N, 17.1133°E, 6.XI.2009, R. Ozimec leg., CBSSC IT2266; 2 ♂♂ Lađena, Mokre noge (cave), 43.2967°N, 17.0906°E, 15.VII.2013, B. Jalžić leg., CBSSC IT3811; 2 ♂♂, 2 ♀♀, Župa, Lozovci, Mravinjuša (cave), 43.3461°N, 17.0998°E, 21.III.2004, J. Bedek leg., CBSSC IT209; 1 ♂, 2 ♀♀, 1 juv., same loclity and date, B. Jalžić leg., CNHM 4/1609; 4 ♂♂, 5 ♀♀, Tučepi, Srida sela, Ravna vlaška, Tučepska vilenjača (cave), 43.2865°N, 17.0836°E, 3.V.1997, R. Ozimec leg., CBSSC IT6; 1 ♀, same data, CBSSC IT7; 2 ♂♂, same locality, 1.IX.1998, F. Gasparo leg., CBSSC IT2632; 1 ♂ juv., same locality, 18.VI.2011, N. Raguž leg., CBSSC IT3159; 2 ♂♂, same locality, 24.VI.2017, M. Pavlek leg., CBSSC IT4084; 2 ♂♂, same locality and date, T. Rožman leg., CBSSC IT4087; 1 ♂, same locality and date, I. Mišerić leg., CBSSC IT4090; 1 ♂, same locality, 30.IV.2012, T. Čuković leg., CBSSC IT4093; 1 ♂, 1 ♀, Mačka, Velika Mačka (cave), 43.2771°N, 17.1311°E, 26.VI.2008, P. Rade leg., CBSSC IT3161; 2 ♂♂, 1 ♀, 1 juv., Zečica, Zečica (cave), 43.2604°N, 17.1462°E, 2.IV.2006, M. Pavlek leg., CBSSC IT489; 3 ♂♂, 1 ♀, 1 juv. same locality, 24.VI.2007, M. Lukić leg., CBSSC IT3143; Imotski: 2 ♂♂, 1 ♀, Imotski, Krstatice, Slivno, Procipnjača (cave), 9.VII.2000, M. Franičević leg., CBSSC IT3032.

Redescription. Maximum length: ♂, 9.8 mm; ♀, 10.2 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon (Figure A.1A). Back smooth, with some triangular scale-setae (Figure A.1B). Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods (Figure A.1D). Eyes absent. Cephalon (Figure A.1C) with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, and pereonites 2–7 progressively more concave (Figure A.1A). Pleonites 3–5 with small posterior points visible in dorsal view (Figure A.1D). Distal part of telson with concave sides and broadly rounded apex (Figure A.1D). Antennula (Figure A.1E) of three articles, distal article flattened and bearing six to 11 aesthetascs. Antenna (Figure A.1F) with distal articles of peduncle smooth; flagellum of seven to 10 articles with one row of aesthetascs on four to six different articles, always on second and third article. Mandibles (Figure A. 2A, B) with one penicil on right and three on left; molar process with one penicil on right and none on left. Outer branch of maxillula (Figure A. 2C) with 5+6 teeth, apically entire, and one slender stalk; inner branch with three penicils, outer and middle subequal, inner distinctly longer. Maxilla (Figure A. 2D) with setose and bilobate apex, lobes subequal in width. Maxilliped (Figure A. 2E) endite narrow, with large segmented apical penicil; palp distally with three rounded lobes, basal article with two small compound setae; basis with rounded outer lobe protruding posteriorly and covered with long setae on margin. Pereopods with large, bifid and setose dactylar seta (Figure A. 3A). Uropod (Figure A.1D) with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male. Pereopod 1 (Figure A. 3A) carpus bearing five to six setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–3 merus with sternal margin straight, pereopods 4–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 3B) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized hump-shaped lobe in proximal part directed ventrally and bearing one seta; carpus with straight sternal and tergal margins. Genital papilla (Figure A. 4A) with rounded apical part. Pleopod 1 (Figure A. 4A) exopod with posterior apex narrowly rounded, slightly concave outer margin, slightly convex inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 4B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in Figure A. 4C–E.

Type locality. Bilek-Höhle in der Südherzegowina (Dejanova pećina, Bileća, Herzegovina) (Verhoeff 1931). The cave is flooded by the Bileća lake hydro accumulation.

Remarks. The type locality is flooded by the Bileća lake hydro accumulation and is no more available for collecting the topotype material. Therefore we tried to collect the material in caves in the surrounding area, unsuccessfully. The closest locality where we were able to collect *A. heroldi* was the cave Jama u Zagrebištu, located around 8 km far from the type locality.

Alpioniscus heroldi is the largest of *heroldi*-lineage species and one of the largest of Dinaric *Illyrionethes* species. The species is characterized by the smooth dorsum, lack of ridges on the posterior margins of somites and the lack of a hump on the tergal margin of the male pereopod 7 carpus. This last character is present also in *A. haasi* (Verhoeff, 1931) and *A. kratochvili* (Frankenberger, 1938) from which it differs by the hump-shaped sternal lobe of pereopod 7 merus directed ventrally, instead of a hook-shaped lobe, directed ventro-laterally (*A. haasi*) or laterally

(*A. kratochvili*). Moreover, from *A. haasi* it differs by the slightly concave, instead of sinuous, outer margin of the male pleopod 1 exopod, . From *A. kratochvili* it also differs by the narrowly instead of broadly rounded, apex of the male pleopod 1 exopod.

The species is amphibious (Sket 1986).

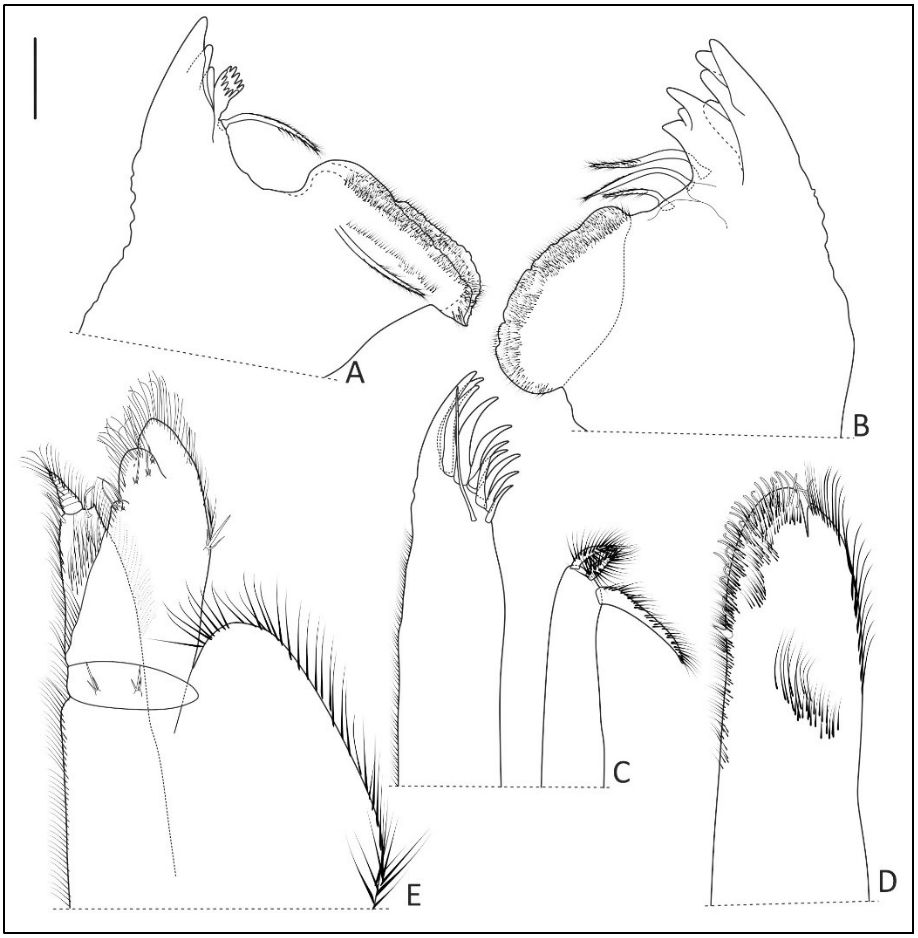


Figure A. 2. *Alpioniscus* (*Illyrionethes*) *heroldi* ♂ CBSSC IT2427 from Jama u Zagrebištu. **A** right mandible; **B** left mandible; **C** maxillula; **D** maxilla; **E** maxilliped. Scale bar: 0.1 mm.

Distribution. Herzegovina, S Dalmatia including the Pelješac peninsula (Figure A. 19).

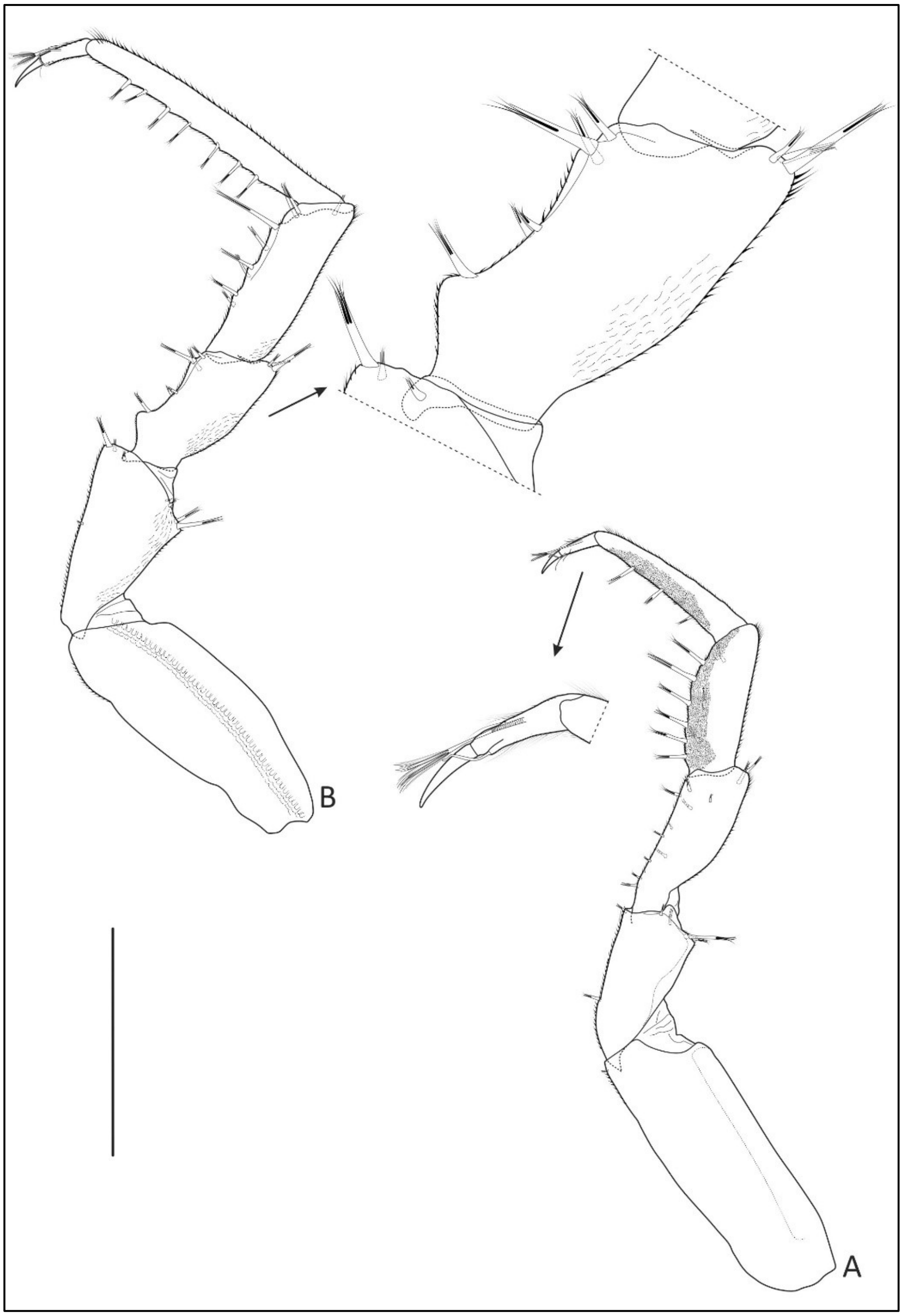


Figure A. 3. *Alpioniscus* (*Illyrionethes*) *heroldi* ♂ CBSSC IT2427 from Jama u Zagrebištu. **A** pereopod 1 with enlargement of dactylus; **B** pereopod 7 rostral view with enlargement of merus. Scale bar: 1 mm.

Alpioniscus* (*Illyrionethes*) *haasi (Verhoeff, 1931)

Figure A. 5, Figure A. 6, Figure A. 19

Illyrionethes haasi Verhoeff 1931b*:* 123, fig. 2.–1931a: 20–23, figs 7, 8.–Frankenberger 1937: 173.–1938: 25, 27, 34, fig. 1.–Strouhal 1939b: 117, map.–1940: 89, 95.–Frankenberger and Strouhal 1940: 448, 450.–Arcangeli 1947: 108.

Alpioniscus (*Illyrionethes*) *haasi*.–Vandel 1946: 155.–Buturović 1955a: 151.–1957: 6, 9, 14, 34, 49, 52, 65, fig. 24.–Schmölzer 1965: 58, fig. 222.–Karaman 1966: 377.–Tabacaru 1996: 35.–Horvatović 2014: 125, 175, 223, 240, fig. 7.28.–Bedek et al. 2019a: 34.–2019b: 491.–2019c: fig. 5.

Alpioniscus hassii.–Potočnik 1989: 64.

Alpioniscus haasi.–Potočnik 1993: 84.–Schmalfuss 2003: 13.–Bedek et al. 2006: 48, 92.–2011: 238, 240, 269, fig. 12.–Jalžić et al. 2010: 20.–2013: 20, 30.–Senckenberg 2018.

Alpioniscus hassi.–Potočnik 1993: 178.

Material examined. CROATIA. **Korčula Island**: 2 ♀♀, Korčula, Pišurka (cave), 42.9594°N, 17.1292°E, 28.VIII.1995, R. Ozimec leg., CBSSC IT1999; 8 ♂♂, 5 ♀♀, same locality, 25.-28.VIII.1997, F. Gasparo leg., CBSSC IT2636; 3 ♂♂, 1 ♀, 1 juv., same locality, 12.II.1998, S. Vujčić-Karlo leg., CBSSC IT2089; 1 ♂, same locality, 23.IV.2004, H. Bilandžija leg., CBSSC IT1994; 2 ♂♂, same locality and date, M. Pavlek leg., CBSSC IT1997; 1 ♂, same locality and date, R. Ozimec leg., CBSSC IT2006; 1 ♀, same locality, 1.X.2007, H. Bilandžija, P. Bregović leg., CBSSC IT2353; 2 ♂♂, 2 ♀♀, 1 juv., same locality and date, H. Bilandžija leg., CBSSC IT2002; 1 ♀, same data, CBSSC IT2084; 1 ♂, same locality, 12.VIII.2008, R. Ozimec leg., CBSSC IT2489; 1 ♀, same locality, 26.XII.2009, M. Ozimec leg., CBSSC IT2085; 1 ♂, 1 ♀, 1 juv., Pupnat, Golubinka 2 (cave), 20.III.2010, A. Kirin leg., CBSSC IT2534; 1 ♀ Čara, Kamena, Jama na Kamenoj (cave), 27.IV.2004, M. Lukić leg., CBSSC IT2338; 1 ♂, 2 ♀♀, same locality and date, B. Jalžić leg., CBSSC IT2339; 2 ♂♂, 2 ♀♀, 1 juv., Lumbarda, Jama na Pudarici (cave), 42.9144°N, 17.1625°E, 17.III.2010, L. Đud leg., CBSSC IT2498; 1 ♂, 6 ♀♀, Pupnat, Duboki dol, Jama u Dubokom dolu (cave), 42.9469°N, 17.0223°E, 27.IV.2004, R. Ozimec leg., CBSSC IT2351; 2 ♂♂, 3 ♀♀, 2 juv., Pupnat, Jama za Dobri dol (cave), 20.III.2010, A. Kirin leg., CBSSC IT2504; 2 ♀♀, 1 juv., Pupnat, Moče (cave), 18.III.2010, T. Rubinić leg., CBSSC IT2495; 1 ♀, same locality and date, A. Kirin leg., CBSSC IT2496; 1 ♂, same locality and date, L. Đud leg., CBSSC IT2497; 1 ♂, 1 juv., Žrnovo, Rankova jama (cave), 21.III.2010, A. Kirin leg., CBSSC IT2530; 1 ♂, 3 ♀♀, 1 juv., Račišće, Samograd, Samograd (cave), 42.9705°N, 16.9960°E, 4.VI.2000, R. Ozimec, S. Gottstein Matočec, M. Vojinović leg., CBSSC IT71; 1 ♀, same locality, 26.IV.2004, M. Pavlek leg., CBSSC IT2345; 1 ♂, same locality and date, H. Bilandžija leg., CBSSC IT2346; 1 ♀, same locality, 30.IX.2007, P. Bregović leg., CBSSC IT2347; 2 juvs, same locality and date, M. Pavlek leg., CBSSC IT2349; 1 ♂, 1 ♀, same locality and date, H. Bilandžija leg., CBSSC IT2353; 1 ♀, same locality, 18.III.2010, R. Ozimec leg., CBSSC IT2500; 2 ♀♀, same locality, 20.III.2010, L. Đud leg., CBSSC IT2502; 3 ♀♀, same locality, 16.IV.2011, R. Ozimec leg., CBSSC IT4468; 2 ♂♂, same locality and date, I. Njunjić leg., CBSSC IT4470; **Pelješac**: 1 ♂, 1 ♀, Orebić, Viganj, Poskokova jama (cave), 43.0013°N, 17.1343°E, 2.VIII.2002, N. Bočić leg., CBSSC IT2981; 1 ♂, Orebić, Viganj, Sv. Ilija; Mali Sopaj, Vanja,Vanjice (cave), 43.0043°N, 17.1346°E, 24.VII.2002, N. Fabac, V. Dubravčić leg., CBSSC IT3000; 1 ♂, 2 ♀♀, 2 juvs, Orebić, Franjvački samostan, Čagjina jama (cave), 42.9774°N, 17.1551°E, 6.IV.2007, M. Pavlek leg., CBSSC IT4423; 1 ♂, 3 ♀♀, 2 juvs, same locality, 14.XI.2018, P. Visković leg., CBSSC IT4424; 2 ♂♂, 5 ♀♀, Janjina, Gorska jama (cave), 42.9270°N, 17.4248°E, 3.XI.2003, R. Ozimec leg., CBSSC IT4430; 1 ♂, 2 ♀♀, same locality and date, I. Jaklinović leg., CBSSC IT4433.

Redescription. Maximum length: ♂, 7.3 mm; ♀, 8.4 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon. Back smooth, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 5A) of three articles, distal article flattened and bearing seven to 10 aesthetascs. Antenna (Figure A. 5B) with distal articles of peduncle smooth; flagellum of nine to 11 articles with one row of aesthetascs on three to five different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

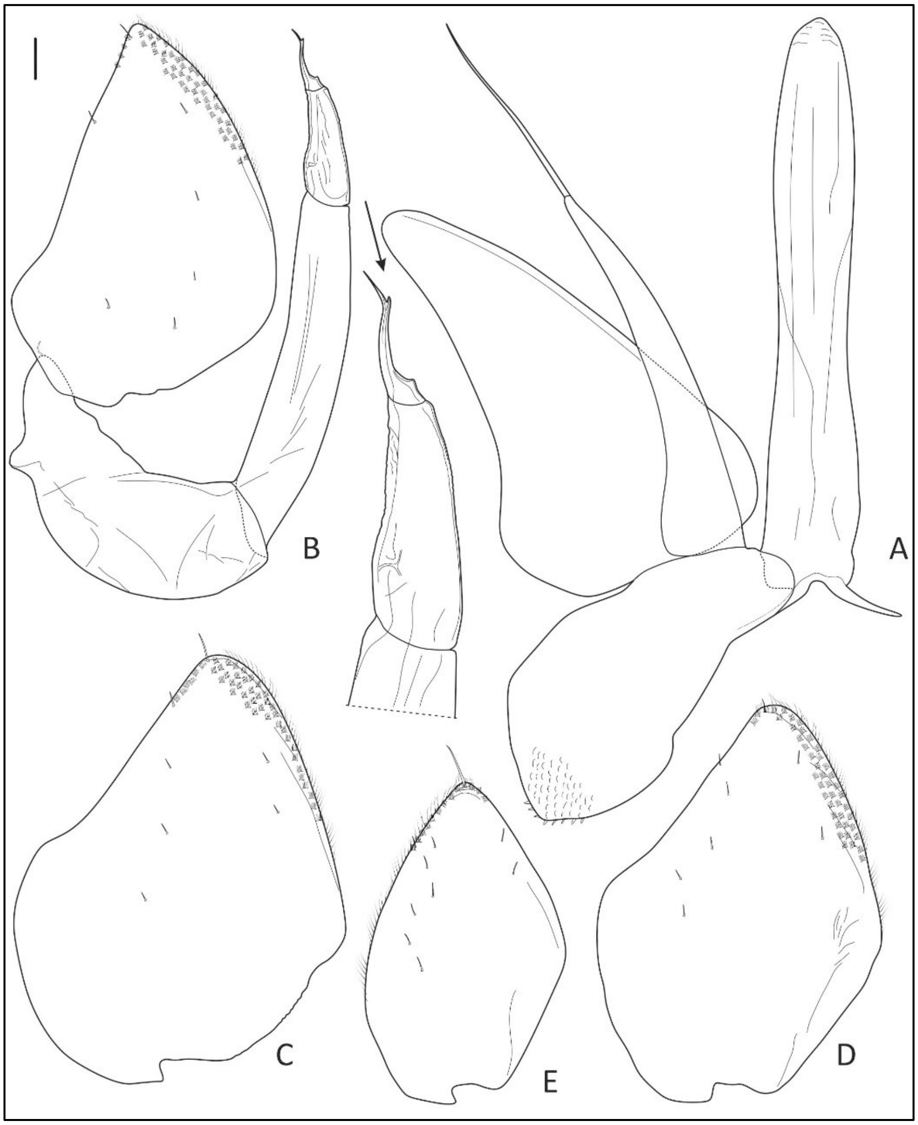


Figure A. 4. *Alpioniscus* (*Illyrionethes*) *heroldi* ♂ CBSSC IT2427 from Jama u Zagrebištu. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip; **C** pleopod 3 exopod; **D** pleopod 4 exopod; **E** pleopod 5 exopod. Scale bar: 0.1 mm.

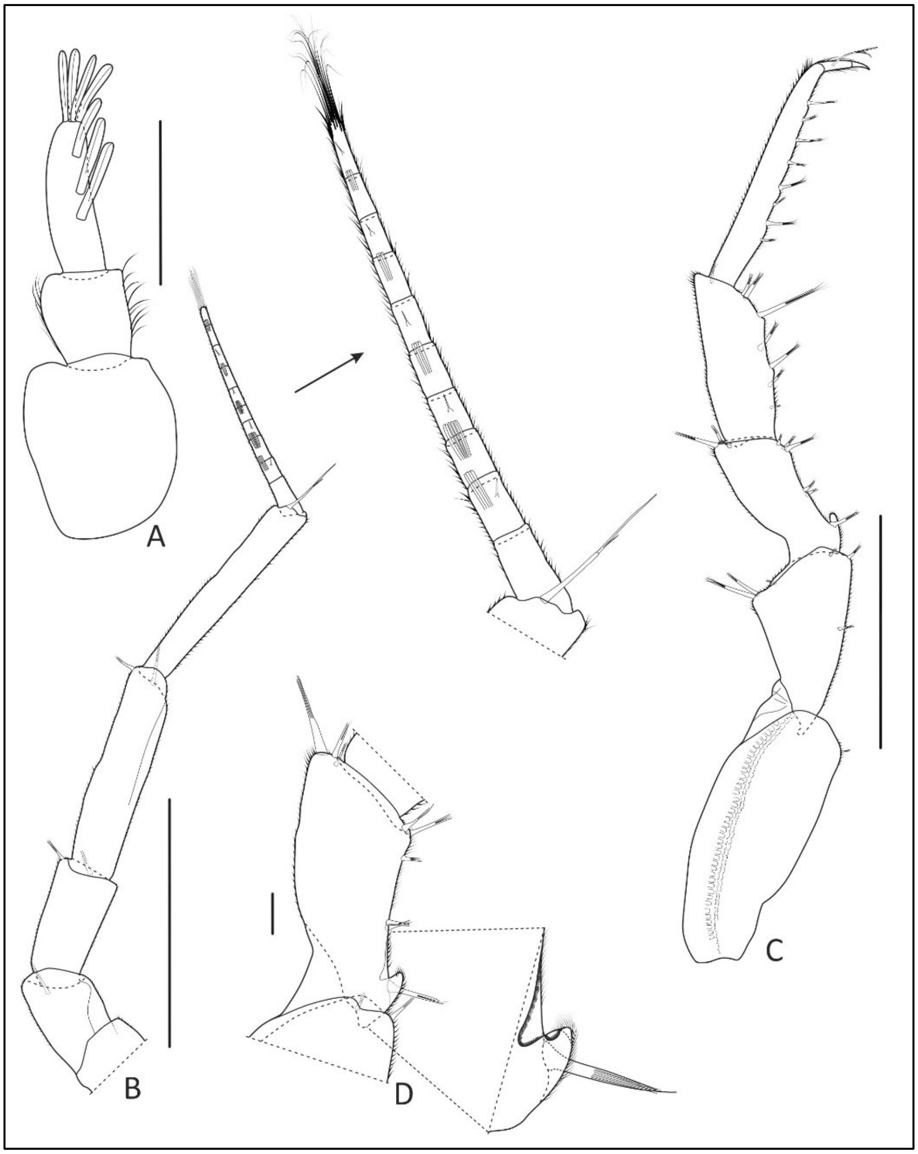


Figure A. 5. *Alpioniscus* (*Illyrionethes*) *haasi* topotype ♂ CBSSC IT1997 from Pišurka. **A** antennula; **B** antenna with enlargement of flagellum; **C** pereopod 7 rostral view; **D** pereopod 7 merus caudal view with enlargement of hook. Scale bars: 0.1 mm (**A, D**), 1 mm (**B, C**).

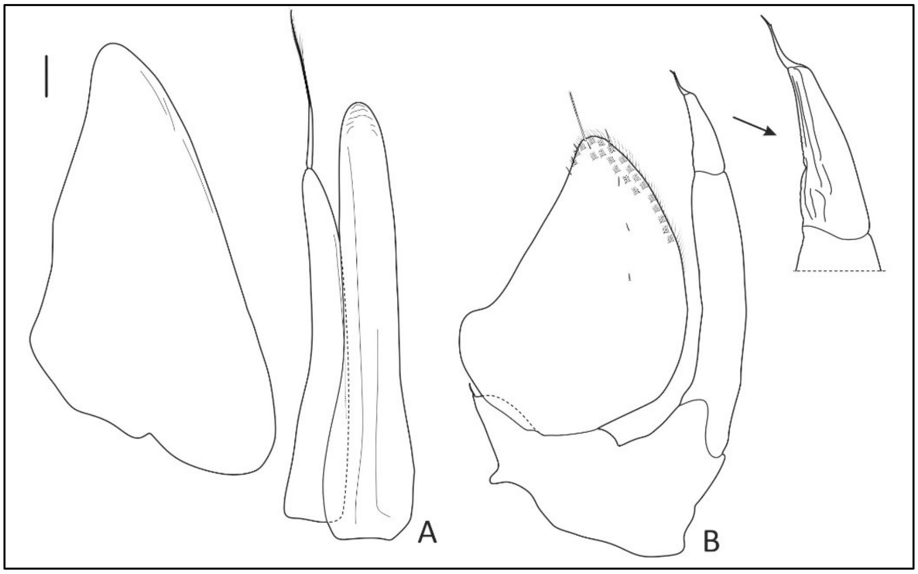


Figure A. 6. *Alpioniscus* (*Illyrionethes*) *haasi* topotype ♂ CBSSC IT1997 from Pišurka. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Male. Pereopod 1 carpus bearing six setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–2 merus with sternal margin straight, pereopods 3–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 5C, D) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized hook-shaped lobe in proximal part directed ventro-laterally and bearing one seta; carpus with straight sternal and almost straight tergal margin. Genital papilla (Figure A. 6A) with rounded apical part. Pleopod 1 (Figure A. 6A) exopod with posterior apex narrowly rounded, sinuous outer margin, slightly convex inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 6B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

Type locality. Insel Curzola in der Paganetti-Höhle (Pišurka, Korčula, Korčula Island, Croatia—cave) (Verhoeff 1931b).

Remarks. The species is characterized by the smooth dorsum, the lack of ridges on the posterior margins of thesomites and the lack of a hump on the tergal margin of the male pereopod 7 carpus.

The last character is present also in *A. heroldi* and *A. kratochvili*, from which it differs by the sinuous outer margin of the male pleopod 1 exopod.

Distribution. The Korčula island and Pelješac peninsula (Figure A. 19).

Alpioniscus* (*Illyrionethes*) *herzegowinensis (Verhoeff, 1931)
Figure A. 7, Figure A. 8, Figure A. 19

Illyrionethes herzegowinensis Verhoeff 1931a: 21, 22; figs 1–3.–Frankenberger 1937: 173.–1938: 25, 28, 34.–Strouhal 1938: 275–277, figs 12, 13.–1939b: 115, 125–127, map.–1939c: 26–28.–1939a: 7, 10–14.–1940: 95.–Frankenberger and Strouhal 1940: 448, 450–451.–Buturović 1951: 98, 102–104.
Illyrionethes heroldi.–Strouhal 1939b: 124 [partim: Lok. 806, "Čelina Jama"; hoch über dem Popovo Polje in Richtung Grepci gelegen].
Illyrionethes (?) *heroldi*.–Strouhal 1939d: 23.
Alpioniscus herzegowinensis.–Vandel 1947: 267, 271.–Potočnik 1989: 64.–Schmalfuss 2003: 13, 14.–Bedek et al. 2011*:* 271 [partim: *nec* Lukina jama – Trojama (cave system), Hajdučki kukovi, Velebit, Krasno].–Orrell and Hollowell 2018.
Alpioniscus (*Illyrionethes*) *herzegowinensis*.–Buturović 1955a: 151.–1957: 9, 14, 20, 23, 34, 49, 52, fig. 24.–Schmölzer 1965: 58, fig. 217.–Karaman 1966: 377.–Potočnik 1993: 85, 178.–Tabacaru 1996: 35.–Horvatović 2014: 176, 223, 240, fig. 7.28.–Karaman and Horvatović 2018: 266.–Bedek et al. 2019b: 491.–2019c: fig. 5.
Alpioniscus (Illyrionethes) verhoeffi.–Horvatović 2014: 125 [partim: Petro-Pavlova pećina].

Material examined. BOSNIA AND HERZEGOVINA. **Herzegovina, Trebinje**: 1 ♂, Bihovo, Doli, Pavlova pećina (cave), 42.6664°N, 18.3077°E, 28.I.2007, J. Bedek leg., CBSSC IT567; 1 ♂ juv., same data, CBSSC IT568, 1 ♂, same data, CBSSC IT570; 1 ♂, same data, CBSSC IT571; 1 ♂, 2 ♀♀, 1 juv., same locality and date, H. Bilandđija leg., CBSSC IT573; 5 ♂♂, 6 ♀♀, same locality, 30.III.2012, M. Lukić leg., CBSSC IT2622; 2 ♂♂, 2 ♀♀, same locality and date, J. Bedek leg., CBSSC IT2623; 1 ♂, 2 ♀♀, same locality and date, A. Komerički leg., CBSSC IT2624; 1 ♂, Vučja pećina (cave), 42.7160°N, 18.3260°E, 27.I.2007, H. Bilandžija leg., CBSSC IT579.

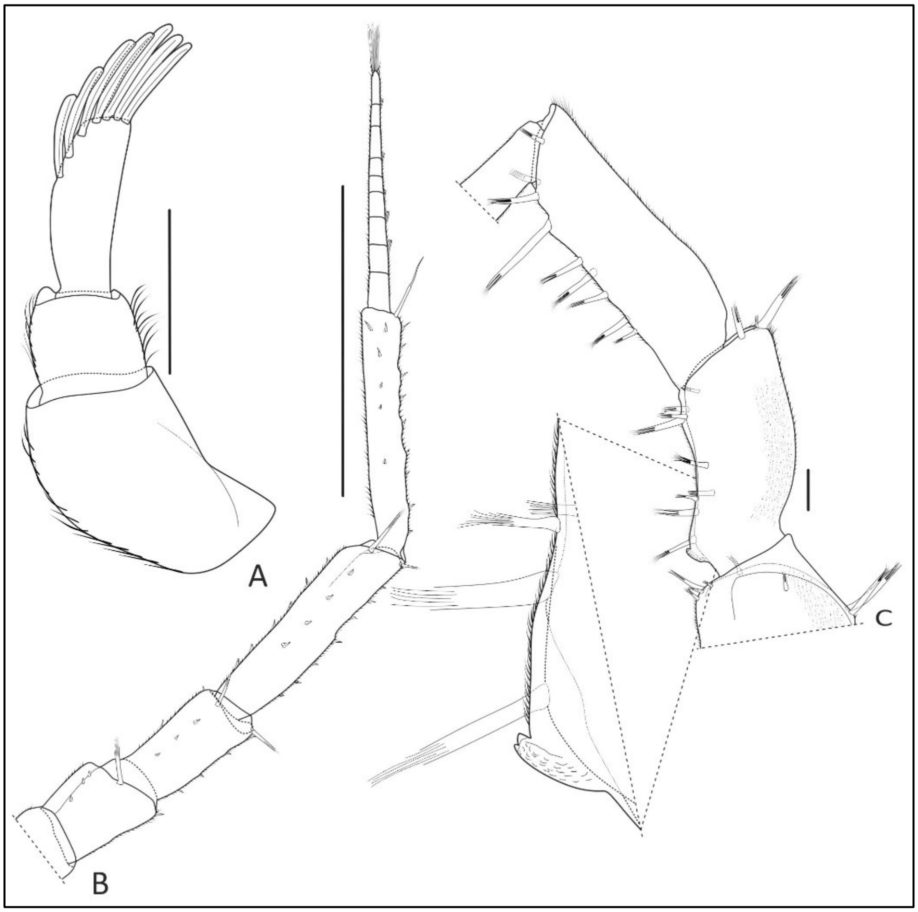


Figure A. 7. *Alpioniscus* (*Illyrionethes*) *herzegowinensis* ♂ CBSSC IT567 from Pavlova pećina. **A** antennula; **B** antenna; **C** pereopod 7 merus and carpus caudal view with enlargement of merus hook. Scale bars: 0.1 mm (**A, C**), 1 mm (**B**).

Redescription. Maximum length: ♂, 5.0 mm; ♀, 7.2 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon. Back smooth, with ridges near posterior margins of cephalon and pereonites 1–3, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5 and. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 7A) of three articles, distal article flattened and bearing seven aesthetascs. Antenna (Figure A. 7B) with distal articles of peduncle granulated; flagellum of eight to nine articles with one row of aesthetascs on three to six different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

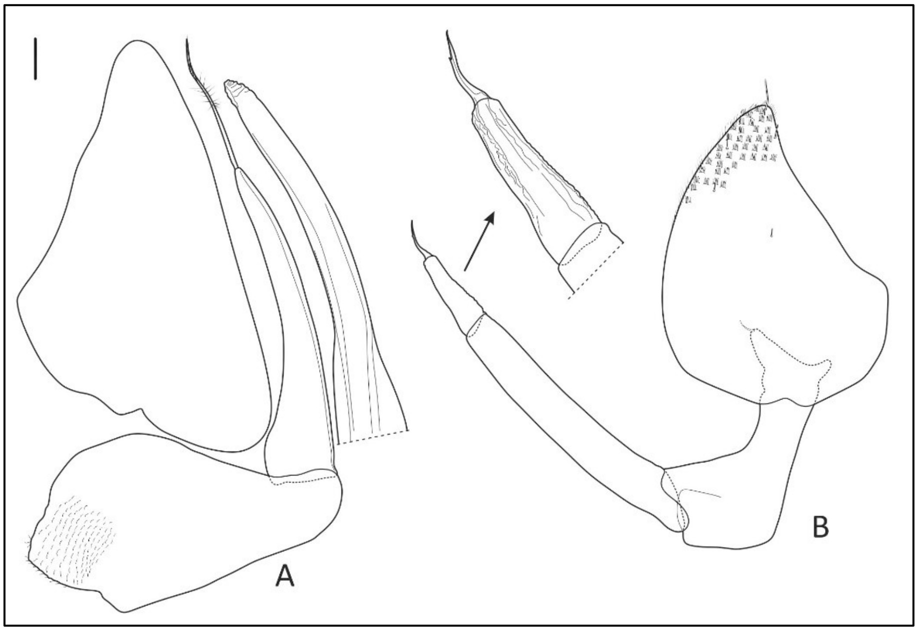


Figure A. 8. *Alpioniscus* (*Illyrionethes*) *herzegowinensis* ♂ CBSSC IT567 from Pavlova pećina. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Male. Pereopod 1 carpus bearing five to six setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–4 merus with sternal margin straight, pereopods 5–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 7C) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized double hump-shaped lobe with crochet in proximal part directed ventrally and bearing one seta; carpus with straight sternal margin and shallow, rounded tergal hump in proximal part. Genital papilla (Figure A. 8A) with rounded apical part. Pleopod 1 (Figure A. 8A) exopod with posterior apex narrowly rounded, sinuous outer margin, straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 8B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

Type locality. Im Gebiet der Schuma der südwestlichsten Herzegowina in verschiedenen Höhlen im Dunkeln (caves in Šuma, Trebinje, Bosnia and Herzegovina) (Verhoeff 1931a).

Remarks. We have tried to collect topotype specimens in the caves of the Šuma area, without success. Not many caves were available for collecting due to minefields in the Šuma area. The closest cave where we were able to collect specimens of *A. herzegowinensis* was Pavlova pećina, around 5 km far from Šuma area.

Alpioniscus herzegowinensis is characterized by the smooth habitus with ridges on the pereonites posterior margins,lack of a hump on the tergal margin of the male pereopod 7 carpus, anda double hump-shaped sternal lobe of pereopod 7 merus, a unique character among the Dinaric *Illyrionethes* species. Another prominent character is the sinuous outer margin of the pleopod 1 exopod (similar only to *A. haasi* and *A. trogirensis* Buturović, 1955), but this character is shown only in the largest males (≥4.5 mm long). In the smaller specimens it is slightly concave, and for this reason they can be easily misidentified.

Distribution. SE Herzegovina (Figure A. 19)

Alpioniscus* (*Illyrionethes*) *kratochvili (Frankenberger, 1938)

Figure A. 9, Figure A. 10, Figure A. 19

Titanethes albus.–Girometta 1914: 15 [partim: jama "Propód"].–Langhoffer 1915: 20 [partim: Jama Propód].

Illyrionethes kratochvili Frankenberger 1938: 32, 33, figs 8, 9.–Strouhal 1939b: 117, map.–1939c: 17.–1940: 95.–Frankenberger and Strouhal 1940: 448–450, plate 6.

Alpioniscus (*Illyrionethes*) *kratochvili*.–Vandel 1946: 155.–Buturović 1955: 135.–1957: 9, 18, 34, 49, fig. 24.–Schmölzer 1965: 60, figs 225, 226.–Karaman 1966: 377.–Potočnik 1989: 85, 178.–Tabacaru 1996: 35.–Horvatović 2014: 126, 175, 176, 223, 240, fig. 7.28.–Bedek et al. 2019a: 34.–2019b: 491.–2019c: fig. 5.

Alpioniscus kratochvili.–Potočnik 1989: 64.–Schmalfuss 2003: 14.–Ubic and Ozimec 2005: 172.–Bedek et al. 2006: 42, 92.–2011: 238, 240, 272, 273, fig. 14.–Jalžić et al. 2010: 20.–2013: 18, 30, 124, fig (not numbered).–Hmura et al. 2014: 77, 82, 83, 89.

Material examined. CROATIA. **Hvar island**: 4 ♀♀, Hvar, Pelegrin, Markova špilja (cave), 43.1906°N, 16.4029°E, 3.IV.2005, J. Bedek leg., CBSSC IT1991; 1 ♀, same locality and date, P. Rade leg., CBSSC IT1992; 1 ♂, 6 ♀♀, same locality, 15.III.2011, J. Bedek leg., CBSSC IT2318; 4 ♀♀, same data, CBSSC IT2319; 1 ♂, 1 juv., Jelsa, Humac, Grapčeva špilja (cave), 43.1342°N, 16.7538°E, 5.V.2011, A. Kirin leg., CBSSC IT2717; 1 ♀, same locality, 3.V.2011, A. Čukušić leg., CBSSC IT2718; 2 ♂♂, Jelsa, Zatražišće, Poljice, Podajruša (cave), 43.1432°N, 16.8423°E, 5.V.2011, M. Malenica leg., CBSSC IT2719; 4 ♂♂, 1 juv., same locality and date, L. Đud leg., CBSSC IT2720.

Redescription. Maximum length: ♂, 7.8 mm; ♀, 8.6 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon. Back smooth, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 9A) of three articles, distal article flattened and bearing seven aesthetascs. Antenna (Figure A. 9B) with distal articles of peduncle smooth; flagellum of nine to 10 articles with one row of aesthetascs on four different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

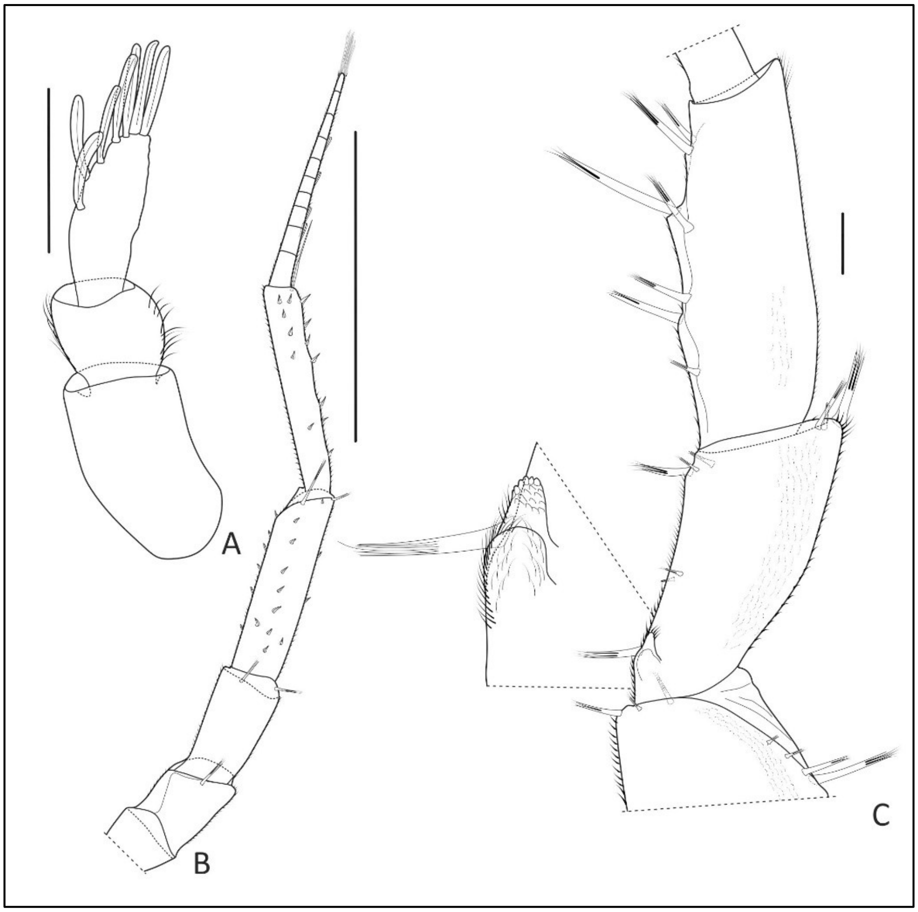


Figure A. 9. *Alpioniscus* (*Illyrionethes*) *kratochvili* topotype ♂ CBSSC IT2318 from Markova špilja. **A** antennula; **B** antenna; **C** pereopod 7 merus and carpus caudal view with enlargement of merus hook. Scale bars: 0.1 mm (**A, C**), 1 mm (**B**).

Male. Pereopod 1 carpus bearing seven setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–4 merus with sternal margin straight, pereopods 5–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 9C) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized hook-shaped lobe in proximal part directed laterally and bearing one seta; carpus with straight sternal and almost straight tergal margin. Genital papilla (Figure A. 10A) with rounded apical part. Pleopod 1 (Figure A. 10A) exopod with posterior apex broadly rounded, slightly concave outer margin, straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 10B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

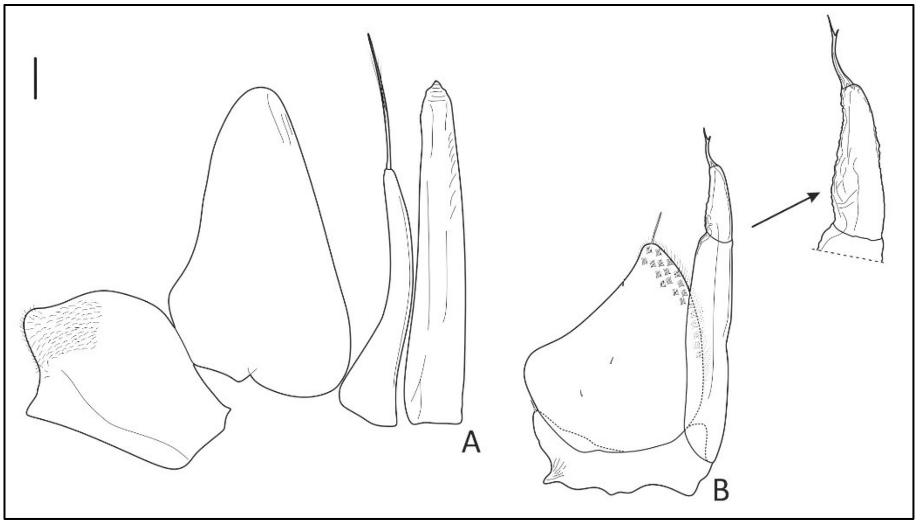


Figure A. 10. *Alpioniscus* (*Illyrionethes*) *kratochvili* topotype ♂ CBSSC IT2318 from Markova špilja. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Type locality. Markova spilja, près de Pellegrino, environs de la ville de Hvar (Markova špilja, Rt. Pelegrin, Hvar, Hvar Island, Croatia—cave); Grćka pećina, environs de la ville de Hvar (Grčka pećina, Hvar, Hvar Island, Croatia—cave); Grabćina spilja près de Gromin Dolac, environs du village de Hum (Grapčeva špilja, Gromin Dolac, Jelsa, Hvar Island, Croatia—cave) (Frankenberger 1938)**.**

Remarks. The species is characterized by the smooth dorsum, lack of ridges on the posterior margins of the somites, and lack of a hump on the tergal margin of the male pereopod 7 carpus, together with *A. haasi* and *A. kratochvili*. From both these species, it differs in having a broadly rounded apex of the male pleopod 1 exopod.

Distribution. Hvar island (Figure A. 19).

Alpioniscus* (*Illyrionethes*) *verhoeffi (Strouhal, 1938)

Figure A. 11, Figure A. 12, Figure A. 19

Illyrionethes verhoeffi Strouhal 1938: 276–278, figs 14–17.–1939b: 117, map.–1940: 95.–Frankenberger and Strouhal 1940: 449, 451.

Alpioniscus (*Illyrionethes*) *verhoeffi*.–Vandel 1946: 155.–Buturović 1955b: 131, 135, map.–1957: 9, 18, 34, 49, fig. 24.–Schmölzer 1965: 59, 60, fig. 223.–Karaman 1966: 378.–Potočnik 1993: 86, 178.–Tabacaru 1996: 36.–Bedek et al. 2019b: 491.–2019c: fig. 5.

Alpioniscus verhoeffi.–Potočnik 1989: 64.–Schmalfuss 2003: 14.–Jalžić et al. 2010: 20.– 2013: 23, 30.–Bedek et al. 2011: 238, 240, 279, 280, 316, fig. 18 [partim: *nec* Špilja na Vršinoj glavici (cave), Stražbenica, Otok, Sinj].–Hlaváč et al. 2019: 92, 97, 98.

? *Alpioniscus verhoeffi*.–Bedek et al. 2011: 279, fig. 18 [partim: Špilja na Vršinoj glavici (cave), Stražbenica, Otok, Sinj].–Horvatović 2014: 125, [partim: BiH: Hercegovina, Bileća, Pećinovac, pećina nad Ravnom gredom; Crna Gora: Nikšić, Studenička pećina]

nec Alpioniscus verhoeffi.– Horvatović 2014: 125 [partim: BiH: Hercegovina, Bihovi, Petro-Pavlova pećina]

Material examined. CROATIA. **Dalmatia, Neretva**: 5 ♂♂, 1 ♀, 3 juvs, Metković, Desne, Varda, Jamica u docima (cave), 43.0663°N, 17.5609°E, 31.IV.2010, A. Kirin leg., CBSSC IT2021; 1 ♂, 2 ♀♀, Ploče, Puljani, Jezero, Kaverna pod vijaduktom kod Puljana (cave), 43.1093°N, 17.4759°E, 23.VI.2010, J. Bedek leg., CBSSC IT2025; 1 ♂, Metković, Bebići, Golovrh, Maica golubinka (cave), 43.1089°N, 17.5664°E, 21.VI.2010, J. Bedek leg., CBSSC IT2023; 1 ♀, same data, CBSSC IT4112; 1 ♂, Desne, Požarova jama (cave), 43.0588°N, 17.5609°E, 25.VIII.1997, B. Jalžić leg., CBSSC IT1157; **Dalmatia, Biokovo**: 1 ♂, 2 juv., Župa, Lozovci, Brikinjava špilja (cave), 43.3452°N, 17.0969°E, 17.XI.2005, R. Ozimec leg., CBSSC IT452; 1 ♂ juv., 1 juv., same locality and date, M. Pavlek leg., CBSSC IT455; 1 ♂, 3 ♀♀, 1 juv., Makarska, Vepric, Bubnjavača (cave), 43.3226°N, 17.0093°E, 3.IV.2006, M. Lukić leg., CBSSC IT493; 1 ♂, same locality and date, J. Bedek leg., CBSSC IT496; 1 ♂, 4 ♀♀, 6 juvs, same locality, 27.X.2006, J. Bedek leg., CBSSC IT732; 3 ♂♂, 2 ♀♀, 1 juv., same locality and date, H. Cvitanović leg., CBSSC IT734; 1 ♂, 7 ♀♀, 2 juvs, same locality, 23.VI.2007, R. Ozimec leg., CBSSC IT3164; 2 ♀♀, same locality and date, J. Bedek leg., CBSSC IT3167; 1 ♂, 2 ♀♀, 1 juv., same locality, 29.VII.2008, R. Ozimec leg., CBSSC IT3172; 2 ♂♂, 1 juv., same locality, 25.VIII.2010, R. Ozimec leg., CBSSC IT2305; 3 ♂♂, 6 ♀♀, same locality, 21.XII.2011, J. Bedek leg., CBSSC IT2481; 1 ♂, 1 ♀, 1 juv., Župa, Gradska spila (cave), 43.3181°N, 17.1176°E, 25.V.2004, H. Cvitanović leg., CBSSC IT214; 1 ♂, 3 ♀♀, 2 juv., same locality and date, B. Jalžić leg., CBSSC IT227; 1 ♂, 1 ♀, same locality, 19.XI.2005, H. Cvitanović leg., CBSSC IT419; 2 ♂♂, 1 ♀, same locality and date, M. Pavlek leg., CBSSC IT421; 1 ♂, same locality and date, R. Ozimec leg., CBSSC IT423; 1 ♂, same locality, 4.IV.2006, H. Bilandžija leg., CBSSC IT426; 1 ♂, 1 ♀, same locality and date, M. Pavlek leg., CBSSC IT428; 2 ♂♂, 3 ♀♀, same locality, 21.VI.2007, M. Lukić leg., CBSSC IT3165; 13 ♂♂, 18 ♀♀, same locality, 8.V.2012, J. Bedek, M. Lukić leg., CBSSC IT2800; 3 ♂♂, 5 ♀♀, Makarska, Bratuš, Jama u Bratušu (cave), 43.3284°N, 16.9794°E, 20.X.2005, R. Ozimec leg., CBSSC IT736; 3 ♂♂, 4 ♀♀, 1 juv., same locality, 27.X.2006, J. Bedek leg., CBSSC IT741; 3 ♂♂, 3 ♀♀, 3 juvs, same locality and date, M. Pavlek leg., CBSSC IT748; 1 ♂, 7 ♀♀, same locality, 20.V.2010, R. Ozimec leg., CBSSC IT2309; 1 ♂, 1 ♀, same locality, 16.XI.2011, H. Cvitanović leg., CBSSC IT2543; 1 ♂, 5 ♀♀, 1 juv., same locality, 8.IV.2007, R. Ozimec leg., CBSSC IT3178; 1 ♂, 6 ♀♀, same locality, 24.VI.2007, R. Ozimec leg., CBSSC IT3181; 1 ♂, Kozica, Jujnovići, Jujnovića špilja (cave), 43.2648°N, 17.1993°E, 2.IV.2006, M. Lukić leg., CBSSC IT485; 1 ♂, 2 ♀♀, 1 juv., same locality and date, R. Ozimec leg., CBSSC IT486; 1 ♂, 2 ♀♀, Baška voda, Bast, Kukor (cave), 43.3568°N, 16.9930°E, 24.IX.2001, R. Ozimec leg., CBSSC IT44; 1 ♂ same locality, 4.XI.2009, R. Ozimec leg., CBSSC IT2271; 1 ♀, 1 juv., same locality, 25.III.2004, J. Bedek leg., CBSSC IT2807; 1 ♂, 1 ♀, Župa, Mala jama (cave), 43.3154°N, 17.1298°E, 27.X.2003, M. Lukić leg., CBSSC IT2806; 2 ♂♂, 21 ♀♀, 5 juvs, Makarska, Bratuš, Mala jama na Pasike (cave), 3.II.2003, T. Rađa leg.; 1 ♂, Župa, Lozovci, Mravinjuša (cave), 43.3461°N, 17.0998°E, 21.III.2004, H. Bilandžija, CBSSC IT231; 1 ♂, 1 ♀, Župa, Samogorska špilja (cave), 43.3183°N, 17.1211°E, 25.V.2004, R. Ozimec leg., CBSSC IT222; 1 ♂, 1 ♀, same locality, 15.XI.2010, H. Cvitanović leg., CBSSC IT2306; 1 ♂, 1 ♀ juv, same locality, 21.VI.2007, R. Ozimec leg., CBSSC IT3142; **Dalmatia, Imotski**: 1 ♂, 1 ♀, 1 juv, Crveno jezero, Balkon prijateljstva (cave), 43.4556°N, 17.1983°E, 3.X.1998, R. Ozimec leg., CBSSC IT3033.

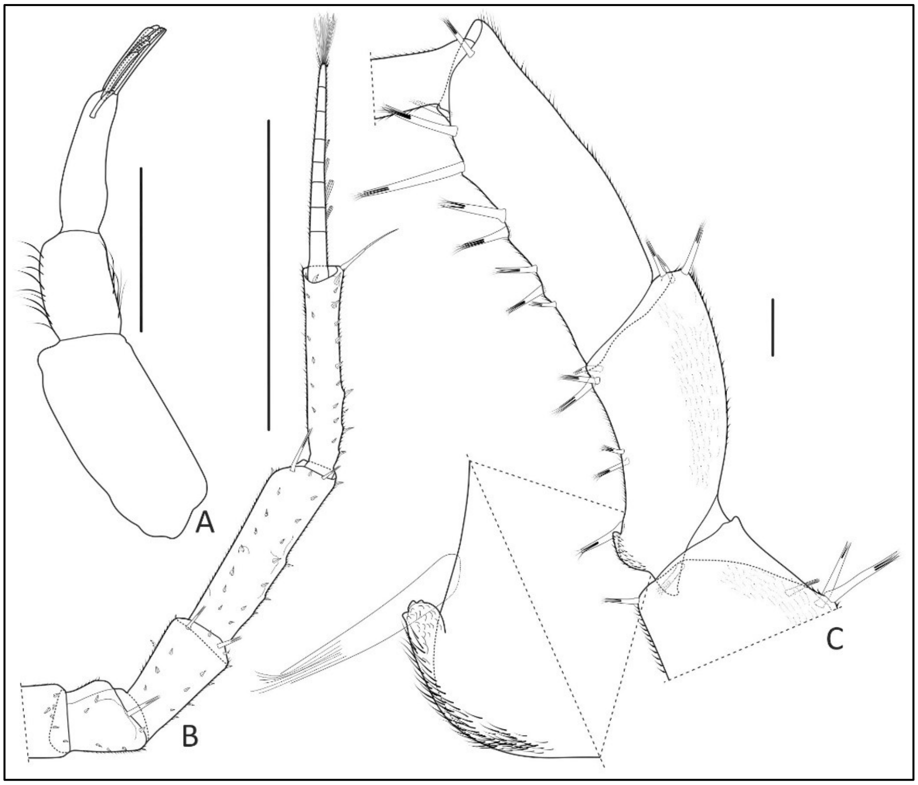


Figure A. 11. *Alpioniscus* (*Illyrionethes*) *verhoeffi* ♂ CBSSC IT2023 from Maica golubinka. **A** antennula; **B** antenna; **C** pereopod 7 merus and carpus caudal view with enlargement of merus hook. Scale bars: 0.1 mm (**A, C**), 1 mm (**B**).

Redescription. Maximum length: ♂, 5.5 mm; ♀, 6.1 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon. Back smooth, with ridges near posterior margins of cephalon and pereonites 1–3, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 11A) of three articles, distal article flattened and bearing nine aesthetascs. Antenna (Figure A. 11B) with distal articles of peduncle slightly granulated; flagellum of six to eight articles with one row of aesthetascs on three to four different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

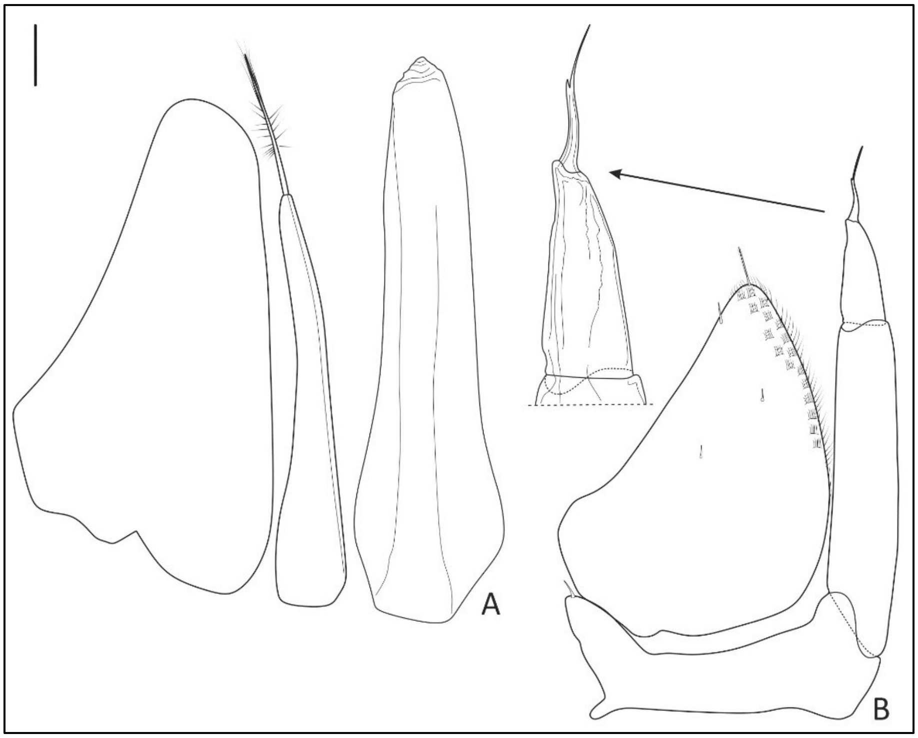


Figure A. 12. *Alpioniscus* (*Illyrionethes*) *verhoeffi* ♂ CBSSC IT2023 from Maica golubinka. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Male. Pereopod 1 carpus bearing five to six setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–2 merus with sternal margin straight, pereopods 3–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 11C) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized hook-shaped lobe in proximal part directed ventro-laterally and bearing one seta; carpus with straight sternal and almost straight tergal margin. Genital papilla (Figure A. 12A) with rounded apical part. Pleopod 1 (Figure A. 12A) exopod with posterior apex broadly rounded, slightly concave outer margin, straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 12B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

Type locality. Narenta-Grotten, Dalmatien (caves in the Neretva river valley, Dalmatia) (Strouhal 1938).

Remarks. The population from Biokovo Mt. shows some small differences, namely the dorsum slightly granulated instead of smooth, more evident in the population near the coast compared to the inner land population. The male carpus 7 has a very shallow, rounded hump on the proximal part of the tergal margin similar to *A. trogirensis* and *A. busljetai*, from which it differs by the shape of pleopod 1 exopod. The pleopod 1 exopod varies from slightly concave to almost straight and, in some specimens, slightly sinuous.

The species is characterized by the smooth dorsum with ridges on the posterior margins of the pereonites and lack of a hump on the tergal margin of the male pereopod 7 carpus, as in *A. herzegowinensis* and *A. drazinai*. From these species, it differs by medium sized ventro-lateral hook of the male pereopod 7 merus, since *A. herzegowinensis* is characterized by a double hump and *A. drazinai* by a large hook directed ventrally.

The citations with '?' are doubtful, and the material from those localities needs to be re-examined with both molecular and morphological analyses.

Distribution. The area from the river Neretva to Biokovo Mt (Figure A. 19).

Alpioniscus* (*Illyrionethes*) *tuberculatus (Frankenberger, 1939)

Figure A. 13, Figure A. 14, Figure A. 19

Illyrionethes tuberculatus Frankenberger 1939: 101–104, figs 4–6.–Strouhal 1940: 95.–Frankenberger and Strouhal 1940: 448–451.

Alpioniscus (*Illyrionethes*) *tuberculatus*.–Buturović 1955b: 134, map.–1957: 34, 49, fig. 24.–Schmölzer 1965: 57, 58, figs 215, 216.–Karaman 1966: 378.–Potočnik 1993: 86, 178.–Tabacaru 1996: 36.–Horvatović 2014: 126, 175, 240, fig. 7.28.–Bedek et al. 2019a: 40.–2019b: 491.–2019c: fig. 5.

Alpioniscus tuberculatus.–Potočnik 1989: 64.–Schmalfuss 2003: 14.

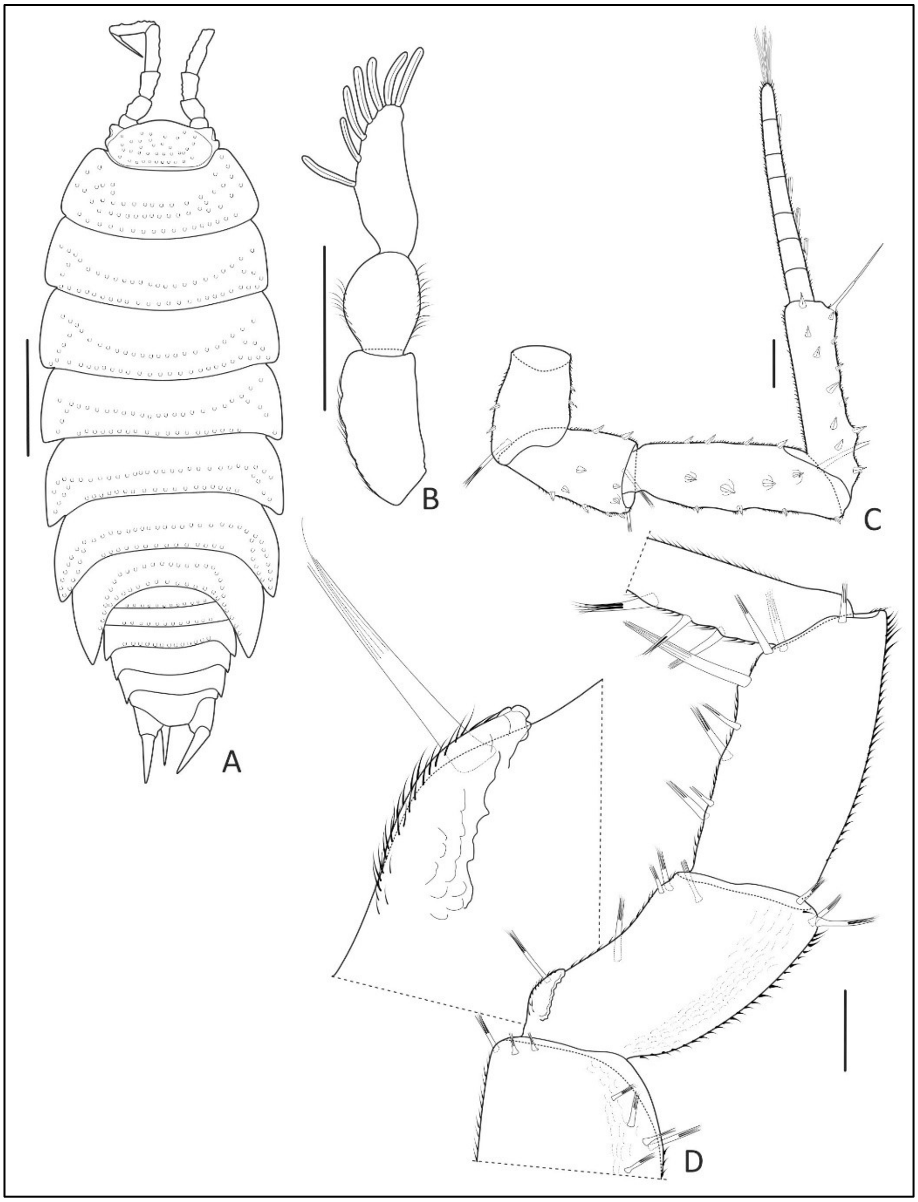


Figure A. 13. *Alpioniscus* (*Illyrionethes*) *tuberculatus* topotype ♀ CBSSC IT1661 from Goranova pećina. **A** habitus in dorsal view. Topotype ♂ CBSSC IT1661 from Goranova pećina. **B** antennula; **C** antenna; **D** pereopod 7 merus and carpus caudal view with enlargement of merus hook. Scale bars: 1 mm (**A**), 0.1 mm (**B**–**D**).

Material examined. BOSNIA AND HETZEGOVINA. **Bosnia, Livno**: 6 ♂♂, 10 ♀♀, Bašajkovac, Duman Spring, Goranova pećina (cave), 43.8323°N, 17.0080°E, 25.VIII.2006, H. Bilandžija leg., CBSSC IT1660; 3 ♂♂, 4 ♀♀, same locality and date, M. Lukić leg., CBSSC IT1661; 4 ♂♂, 5 ♀♀, same locality and date, M. Pavlek leg., CBSSC IT1662; 5 ♀♀, same data, CBSSC IT1663.

Redescription. Maximum length: ♂, 4.5 mm; ♀, 5.6 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon (Figure A. 13A). Back strongly granulated, with ridges near posterior margins of cephalon, pereonites and pleonites 1–3, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 13B) of three articles, distal article flattened and bearing six to seven aesthetascs. Antenna (Figure A. 13C) with distal articles of peduncle granulated; flagellum of seven articles with one row of aesthetascs on four different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male. Pereopod 1 carpus bearing five setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–5 merus with sternal margin straight, pereopod 6 merus with slightly concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 13D) ischium with straight sternal margin; merus with slightly concave sternal margin and medium-sized hook-shaped lobe in proximal part directed laterally and bearing one seta; carpus with straight sternal and almost straight tergal margin. Genital papilla (Figure A. 14A) with rounded apical part. Pleopod 1 (Figure A. 14A) exopod with posterior apex broadly rounded, slightly concave outer margin, slightly convex inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 14B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

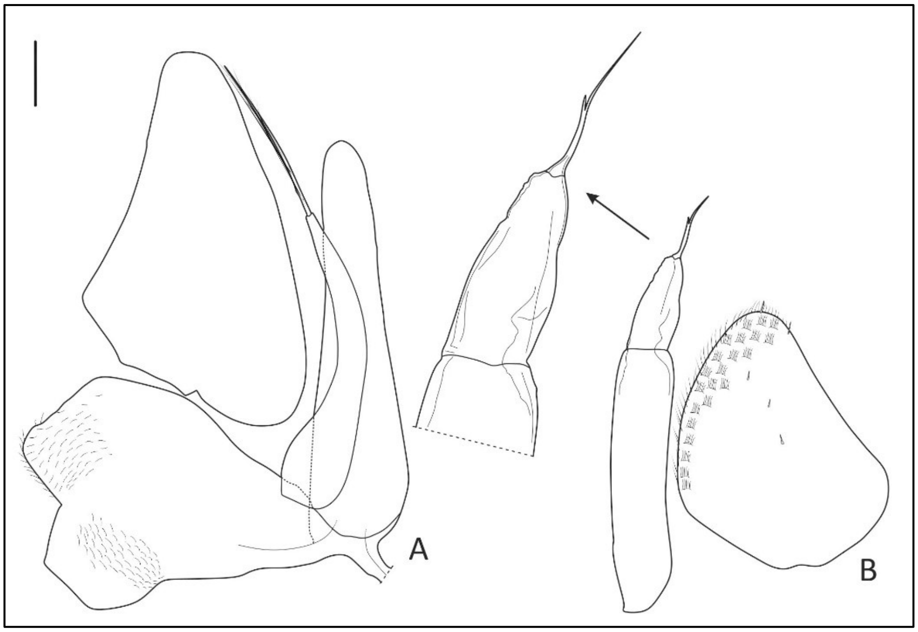


Figure A. 14. *Alpioniscus* (*Illyrionethes*) *tuberculatus* topotype ♂ CBSSC IT1661 from Goranova pećina. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Type locality. Höhle bei Livno (Pećina pri izvoru, Lok. Nr. 269) in Westbosnien (Goranova pećina, izvor Duman, Livno, Bosnia and Herzegovina) (Frankenberger 1939).

Remarks. The species is characterized by strong tegument granulation, unique within Dinaric *Illyrionethes.* The pereopod 7 carpus lacks hump, and merus lobe is hook-shaped, directed laterally. The outer margin of the pleopod 1 exopod is slightly concave, and apex is broadly rounded, similar to *A. busljetai* and, to some extent, to A. *verhoeffi.*

Distribution. Single site endemic species, Livno area (Figure A. 19).

Alpioniscus* (*Illyrionethes*) *absoloni (Strouhal, 1939)
Figure A. 15, Figure A. 16, Figure A. 19

Illyrionethes absoloni Strouhal 1939a: 183–185, figs 4–6.–1939c: 116, 125, 127, map.–1939d: 18, 25.–1939b: 6.–Frankenberger and Strouhal 1940: 450, 452.–Buturović 1951: 104.

Alpioniscus (*Illyrionethes*) *absoloni*.–Vandel 1946: 155.–1947: 271.–Buturović 1957: 18, 34, 37, fig. 24.–Potočnik 1993: 82, 178.–Tabacaru 1996: 14, 16, 20.–Horvatović 2014: 125, 178, 224, 240, fig. 7.28.–Bedek et al. 2017: 213.–2019b: 489.–2019c: fig. 5.

Alpioniscus absoloni.–Potočnik 1989: 64.–Schmalfuss 2003: 13.

Alpioniscus* (*Illyrionethes*) *absoloni absoloni (Strouhal, 1939)

Figure A. 19

Illyrionethes absoloni Strouhal 1939a: 183–185, figs 4–6.–1939c: 116, 125, 127, map.–1939b: 6.–Frankenberger and Strouhal 1940: 450, 452.

Illyrionethes absoloni absoloni Strouhal 1939b: 7.–1940: 89, 95.–Vandel 1946: 160.

Alpioniscus (*Illyrionethes*) *absoloni absoloni*.–Vandel 1946: 160.–Buturović 1957: 7, 9, 14, 49.–Schmölzer 1965: 58, 59, fig. 220.–Karaman 1966: 376.–Potočnik 1993: 82, 83, 178.–Tabacaru 1996: 16.–Bedek et al. 2019c.

Alpioniscus (*Illyrionethes*) *apsoloni apsoloni*.–Buturović 1955b: 135.

Alpioniscus absoloni absoloni.–Potočnik 1989: 69.

Material examined. BOSNIA AND HERZEGOVINA. **Herzegovina, Nevesinje**: 1 ♂, Bišina, Grebak, Novakuša (cave), 43.2488°N, 18.0766°E, 25.VIII.2007, J. Bedek leg., CBSSC IT2013; 1 ♀, same locality, 21.IV.2010, M. Lukić leg., CBSSC IT2014; 2 ♂♂, Kifino Selo, Šniježnica (cave), 24.VII.1963, Deeleman leg., CBSSC IT2014; 5 ♂♂, 1 ♀, same data, SMNS 5190; **Herzegovina, Bileća**: 1 ♂, Granica, Jama u Zagrebištu (cave), 42.9198°N, 18.3491°E, 4.IX.2011, J. Bedek leg., CBSSC IT2426; 1 ♂, Tuhor, Pećina na Tuhoru (cave), 42.8721°N, 18.3929°E, 27.I.2007, J. Bedek leg., CBSSC IT575; 1 ♂, same locality, 26.VIII.2007, J. Bedek leg., CBSSC IT2030; 3 ♂♂, 2 ♀♀, 1 juv., Mirilović, Rogošina 1 (cave), 42.8379°N, 18.3866°E, 21.IV.2010, A. Komerički leg., CBSSC IT2043; 3 ♂♂, 1 ♀ juv., Torić, Vodena gradina, Ujkova jama (cave), 42.8663°N, 18.4029°E, 20.IV.2010, A. Kirin leg., CBSSC IT2033; 15 ♂♂, 11 ♀♀, 5 juvs, same locality and date, J. Bedek leg., CBSSC IT2035; 7 ♂♂, 5 ♀♀, 1 juv., same data, CBSSC IT2037; 3 ♂♂, same locality and date, M. Lukić leg., CBSSC IT2039.

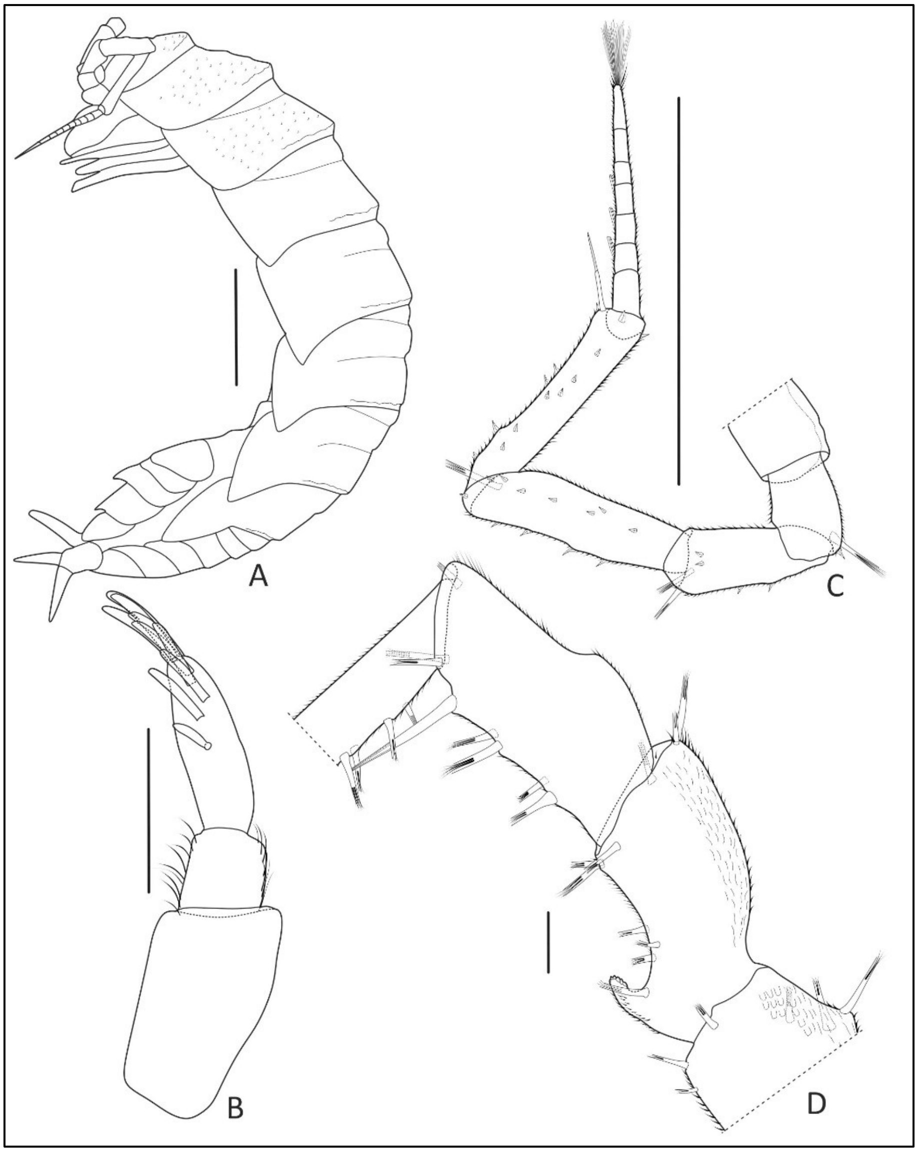


Figure A. 15. *Alpioniscus* (*Illyrionethes*) *absoloni absoloni* ♀ CBSSC IT2014 from Novakuša pećina. **A** habitus in dorsal view. ♂ CBSSC IT2013 from Novakuša pećina. **B** antennula; **C** antenna; **D** pereopod 7 merus and carpus rostral view. Scale bars: 1 mm (**A, C**), 0.1 mm (**B, D**).

Type locality. Lok. 961 der "Biospeologica balcanica", tiefe Jama unter dem Grebah-Sattel am Nevesinjsko Polje (cave under Grebak saddle, Nevesinjsko polje, Nevesinje, Bosnia and Herzegovina) (Strouhal 1939a)

Alpioniscus* (*Illyrionethes*) *absoloni assimilis (Strouhal, 1939)

Figure A. 19

Illyrionethes absoloni assimilis Strouhal 1939a: 187, 188, figs 9, 10.–1939c: 116, 127, map.–1939b: 6, 7.–1940: 89, 95.–Frankenberger and Strouhal 1940: 450.

Alpioniscus (*Illyrionethes*) *absoloni assimilis*.–Buturović 1957: 7, 9, 14, 34, 37, 49, fig. 24.–Schmölzer 1965: 58, 59.–Karaman 1966: 376.–Potočnik 1993: 83, 178.–Tabacaru 1996: 16.–Horvatović 2014: 178, 224.–Karaman and Horvatović 2018: 276.–Bedek et al. 2019c.

Alpioniscus absoloni assimilis.–Potočnik 1989: 69.

Material examined. BOSNIA AND HERZEGOVINA. **Herzegovina, Visočica**: 1 ♂, 5 ♀♀, Glavatičevo, Grušča, Kulina, Čavkarica (cave), 43.5813°N, 18.1601°E, 16.VIII.2010, J. Bedek leg., CBSSC IT2285; 1 ♂ juv., same data, CBSSC IT2383; 5 ♀♀, same locality and date, M. Lukić leg., CBSSC IT2286; 1 ♂ juv., 1 juv., same data, CBSSC IT2382.

Type locality. Lok. 933, der senkrechte Abgrund "Jama pod Mačketom, Visočica Planina, westlich von Ljeljen (1864 m M.-H.) (Jama pod Mačketom, Ljeljen, Visočica Mt., Bosnia and Herzegovina) and Lok 938, "Pečina za Pleskovači", Visočica Planina ("Poćina za Pleskovači, Visočica Mt., Bosnia and Herzegovina) (Strouhal 1939a)

Alpioniscus* (*Illyrionethes*) *absoloni politus (Strouhal, 1939)

Figure A. 19

Illyrionethes absoloni politus Strouhal 1939a: 185, 186, figs 7, 8.–1939c: 116, 127, map.–1939b: 6, 7.–1940: 89, 95.–Frankenberger and Strouhal 1940: 450.

Alpioniscus (*Illyrionethes*) *absoloni politus*.–Vandel 1946: 161.–Buturović 1957: 7, 9, 14, 34, 37, 49, fig. 24.–Schmölzer 1965: 58, 59.–Karaman 1966: 376.–Potočnik 1993: 83, 178.–Tabacaru 1996: 16.–Horvatović 2014: 178, 224.–Bedek et al. 2019c.

Alpioniscus (*Illyrionethes*) *apsoloni politus*.–Buturović 1955b: 134, 135, map.

Alpioniscus absoloni politus.–Potočnik 1989: 69.

Material examined. BOSNIA AND HERZEGOVINA. **Herzegovina, Jablanica**: 10 ♂♂, 20 ♀♀, Donja Jablanica, Višnja, Rudnik na Višnji (mine), 43.6321°N, 17.7515°E, 28.VIII.2007, J. Bedek leg., CBSSC IT2010; 11 ♀♀, same locality and date, M. Lukić leg., CBSSC IT2011; 11 ♀♀, same data, CBSSC IT2012.

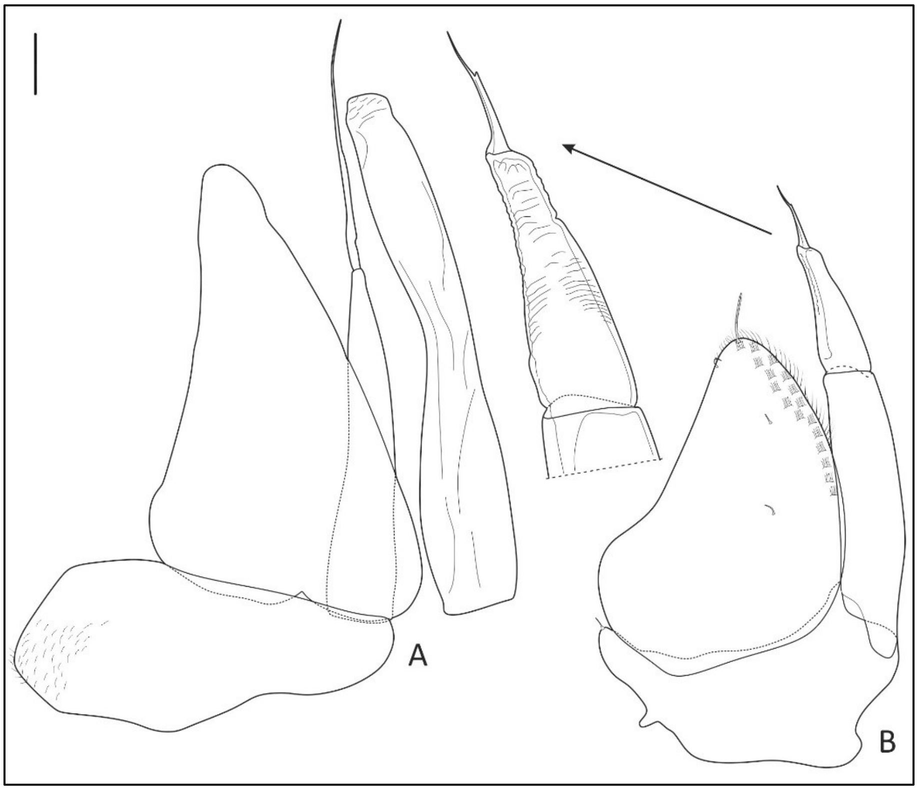


Figure A. 16. *Alpioniscus* (*Illyrionethes*) *absoloni absoloni* ♂ CBSSC IT2013 from Novakuša pećina. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Type locality. Lok. 978, Pečina bei "Dolnja Jablanica", Narenta-Gebiet, ca. 600 m M.-H. (cave near Donja Jablanica, Neretva, Bosnia and Herzegovina) (Strouhal 1939a)

Redescription. Maximum length: ♂, 5.2 mm; ♀, 7.5 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon (Figure A. 15A). Back more or less slightly granulated, with ridges near posterior margins of cephalon and pereonites, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5, telson and uropodal protopods. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites

3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 15B) of three articles, distal article flattened and bearing six to nine aesthetascs. Antenna (Figure A. 15C) with distal articles of peduncle slightly granulated; flagellum of six to eight articles with one row of aesthetascs on three to four different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male. Pereopod 1 carpus bearing five setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–4 merus with sternal margin straight, pereopods 5–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 15D) ischium with straight sternal margin; merus with slightly concave sternal margin and large hook-shaped lobe in proximal part directed ventrally and bearing one seta; carpus with straight sternal and large more or less rounded dorsal hump in proximal part. Genital papilla (Figure A. 16A) with rounded apical part. Pleopod 1 (Figure A. 16A) exopod with posterior apex narrowly rounded, slightly concave outer margin, almost straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 16B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

Remarks. The analyses of available material did not reveal morphological differences between different populations described as subspecies by Strouhal (1939a), slightly higher morphological diversity within populations. This is not in concordance with the results of molecular analyses, which clearly separates the three populations (Bedek et al. 2019c). More material should be analysed, both morphologically and molecularly, to resolve the status of subspecies.
The species is characterized by more or less granulated tegument, with ridges on the pereonites posterior margins. The hump on the pereopod 7 carpus is similar only to *strasseri*-lineage species, from which it differs by the slightly concave outer margin of the pleopod 1 exopod.

Distribution. Herzegovina (Figure A. 19).

Alpioniscus* (*Illyrionethes*) *trogirensis Buturović, 1955

Figure A. 17–Figure A. 18, Figure A. 19

Alpioniscus (*Illyrionethes*) *trogirensis* Buturović 1955a: 150, 151, figs 12, 13.–1957: 8, 9, 37, 49, fig. 24.–Karaman 1966: 378.–Potočnik 1993: 86, 178.–Tabacaru 1996: 36.–Bedek et al. 2019a: 34, 40.–2019c: fig. 5.

Alpioniscus trogirensis.–Potočnik 1989: 64.–Schmalfuss 2003: 14.–Bedek et al. 2006: 72, 92.–2011: 238, 241, 278, fig. 17 [in part *nec* Špilja Sv. Filipa i Jakoba (cave), Marina, Trogir].–Jalžić et al. 2010: 20.–2013: 23, 30.

? *Alpioniscus trogirensis*.–Bedek et al. 2011: 238, 241, 278, fig. 17 [in part Špilja Sv. Filipa i Jakoba (cave), Marina, Trogir]

Material examined. CROATIA. **Dalmatia, Čiovo Island**: 1 ♀, Trogir, Sv. Ante Monastery, Špilja od Bilosoja (cave), 43.5123°N, 16.2607°E, 8.V.2005, M. Lukić leg., CBSSC IT321; 1 ♂, 1 ♀, same locality and date, J. Bedek leg., CBSSC IT322; 3 ♀♀, same locality and date, R. Ozimec leg., CBSSC IT1659; 4 ♀♀, same locality, 5.VIII.2007, M. Pavlek leg., CBSSC IT1658; 4 ♂♂, 6 ♀♀, 1 juv., same locality, 1.V.2010, J. Bedek leg., CBSSC IT2015; 1 ♂, 1 ♀, same data, CBSSC IT2016; 2 ♂♂, 1 ♀, 1 juv., same locality and date, M. Lukić leg., CBSSC IT2017; 10 ♂♂, 3 ♀♀, same locality and date, A. Kirin leg., CBSSC IT2018; 1 ♂, 1 ♀, Trogir, Žedno, Maravića jama (cave), 43.5015°N, 16.2982°E, 1.X.2011, P. Bregović leg., CBSSC IT4310; 2 ♂♂, 1 ♀, same data, CBSSC IT4311; 1 ♂, 1 ♀, same data, CBSSC IT4312; 2 ♂♂, 2 ♀♀, same data, CBSSC IT4313; **Dalmatia, Šolta Island**: 5 ♂♂, 9 ♀♀, Grohote, Vela Straža, Jama na Benkotovu (cave), 43.3757°N, 16.2721°E, 10.VI.2016, T. Dražina leg., CBSSC IT3825; 1 ♀, same data, CBSSC IT3827; 1 ♂, same locality and date, P. Novina leg., CBSSC IT3830; 1 ♀, same locality and date, M. Čuček leg., CBSSC IT3831; 2 ♀♀, same locality and date, L. Kekelj leg., CBSSC IT3833; 3 ♂♂, 3 ♀♀, same locality, 3.VIII.2014, T. Dražina leg., CBSSC IT4314; 12 ♂♂, 10 ♀♀, same locality, 27.VI.2017, M. Pavlek, T. Rožman leg., CBSSC IT4317; 1 ♂, 1 ♀, Gornje Selo, Koludrovi doci, Koludrova špilja (cave), 43.3632°N, 16.3328°E, 28.VI.2017, T. Rožman leg., CBSSC IT4320; 3 ♂♂, 2 ♀♀, Makalina jama (cave), 7.XI.2012, T. Rađa leg., CBSSC IT3274; 3 ♂♂, 2 ♀♀, same data; 1 ♂, 1 ♀, Nečujam, Piškera (cave), 43.3770°N, 16.3162°E, 11.VI.2016, P. Novina leg., CBSSC IT3840; 1 ♂, same locality and date, K. Cindrić leg., CBSSC IT3841; 4 ♂♂, 1 ♀, same locality, 1.VIII.2014, T. Dražina leg., CBSSC IT4318; 1 ♂, 1 ♀, same data, CBSSC IT4319.

Redescription. Maximum length: ♂, 3.7 mm; ♀, 5.5 mm. Colourless body, pereon with almost parallel sides, pleon narrower than pereon. Back slightly granulated, with ridges near posterior margins of cephalon and pereonites, with some triangular scale-setae. Some gland pores on lateral margins of pleonites 4 and 5 and telson. Eyes absent. Cephalon with suprantennal line bent downwards; antennal lobes rounded. Posterior margin of pereonite 1 convex, of pereonites 2, 3 straight, and 4–7 progressively more concave. Pleonites 3–5 with small posterior points visible in dorsal view. Distal part of telson with concave sides and broadly rounded apex. Antennula (Figure A. 17A) of three articles, distal article flattened and bearing six to seven aesthetascs. Antenna (Figure A. 17B) with distal articles of peduncle granulated; flagellum of five to seven articles with one row of aesthetascs on two to three different articles, always on second and third article. Mouthparts as in *A. heroldi*. Pereopods with large, bifid and setose dactylar seta. Uropod with protopod slightly grooved on outer margin; endopod distinctly shorter than exopod, proximally inserted.

Male. Pereopod 1 carpus bearing four to five setae. Pereopod 1 and 2 with propodus and carpus bearing numerous short scales on rostral surface. Pereopods 1–4 merus with sternal margin straight, pereopods 5–6 merus with progressively more concave sternal margin and small lobe proximally. Pereopod 7 (Figure A. 17C) ischium with straight sternal margin; merus with slightly concave sternal margin and small hook-shaped lobe in proximal part directed laterally and bearing one seta; carpus with straight sternal and shallow and long rounded tergal hump in proximal part. Genital papilla (Figure A. 18A) with rounded apical part. Pleopod 1 (Figure A. 18A) exopod with posterior apex narrowly rounded, sinuous outer margin, almost straight inner margin; endopod narrow with almost parallel sides, armed with long apical seta. Pleopod 2 (Figure A. 18B) exopod triangular with slightly concave outer margin; endopod of two articles, distinctly longer than exopod, posterior part narrower than anterior with strong bifid terminal seta. Pleopod 3–5 exopods as in *A. heroldi*.

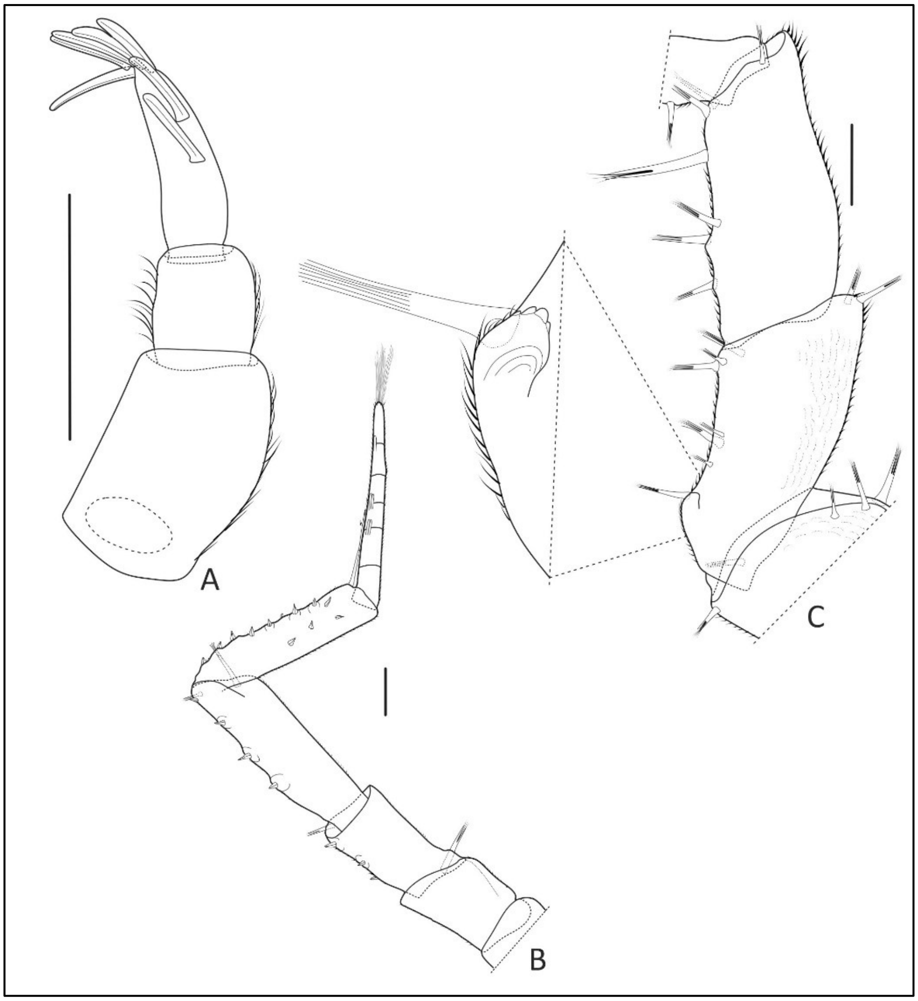


Figure A. 17. *Alpioniscus* (*Illyrionethes*) *trogirensis* topotype ♂ CBSSC IT2015 from Špilja od Bilosoja. **A** antennula; **B** antenna; **C** pereopod 7 merus and carpus caudal view with enlargement of merus hook. Scale bars: 0.1 mm.

Type locality. Grotte près de la ville Trogir (Dalmatie) (Buturović 1955a)**.** According to Hadži (1933) the material collected in 1924 by Stanko Karaman, labelled as »pećina u neposrednoj blizini Trogira« (Grotte près de la ville Trogir, Cave near Trogir) is from one of two caves: "pećina Sv. Filipa i Jakoba kod Marine nedaleko Trigira" (present known as Špilja Sv. Filipa i Jakova, Marina, Trogir) or "pećina kod samostana u samom Trogiru" (present known as Špilja od Bilosoja, St Anthony's Monastery, Čiovo, Trogir). The examined material from the cave Špilja od Bilosoja entirely fits the Buturović species description, unlike the one from the cave Špilja Sv. Filipa i Jakova. Therefore we conclude that the type locality should be the cave Špilja od Bilosoja, and not both caves as reported by Bedek et al. (2011).

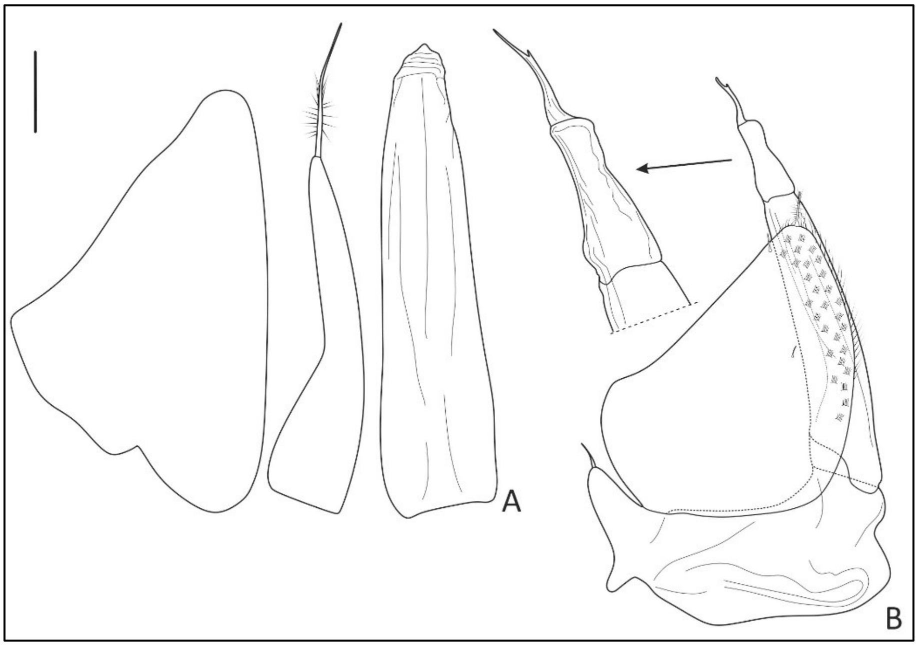


Figure A. 18. *Alpioniscus* (*Illyrionethes*) *trogirensis* topotype ♂ CBSSC IT2015 from Špilja od Bilosoja. **A** genital papilla and pleopod 1; **B** pleopod 2 with enlargement of endopod tip. Scale bar: 0.1 mm.

Remarks. *Alpioniscus trogirensis* is one of the smallest species of Dinaric *Illyrionethes*, characterized by the granulated dorsum. The small hump on pereopod 7 carpus is similar only to those of *A. busljetai* and *A. verhoeffi* Biokovo population. It differs from both by the wide basal part and sinuous outer margin of the pleopod 1 exopod.
The citation with '?' is doubtful, and the material from this locality needs to be re-examined with both molecular and morphological analyses.

Distribution. The islands of Čiovo and Šolta (Figure A. 19).

***Alpioniscus* (*Illyrionethes*) *busljetai* Bedek, Gottstein, Taiti, 2019**
Figure A. 19

Alpioniscus sp.–Bregović et al. 2008: 109 [partim: Markova špilja].

Alpioniscus (*Illyrionethes*) sp. 3.–Bedek et al. 2019c: fig. 5.

Alpioniscus (*Illyrionethes*) *busljetai* Bedek et al. 2019a: 35–41, figs 1–6.

Material examined. **Holotype:** ♂ Croatia, Starigrad Paklenica, Seline, Markova špilja (cave), 44°16.79'N, 15°28.63'E, 30.IX.2008, D. Hmura leg., CBSSC IT4252. **Paratypes:** 1 ♂, 1 ♀, 1 juv., same data as holotype, CBSSC IT2407; 1 ♀, 1 juv., ibid., 5.VI.2006, H. Bilandžija leg., CBSSC IT560; 2 ♂♂, 1 ♀, ibid., 5.VI.2006, M. Pavlek leg., CBSSC IT561; 2 ♂♂, 2 ♀♀, ibid., 1.V.2010, A. Kirin leg., CBSSC IT2235; 1 ♂ juv., ibid., M. Lukić leg., CBSSC IT3975; 1 ♂ juv., ibid., 18.XII.2012, A. Komerički leg., CBSSC IT2881; 1 ♀, ibid., 18.III.2013, K. Miculinić leg., CBSSC IT3974; 1 ♂, 1 ♀, 1 juv., ibid., 20.V.2018, P. Bregović leg., MZUF 9894; 3 ♂♂, 4 ♀♀, ibid., 20.V.2018, N. Kuharić leg., CBSSC IT4250; 2 ♀♀ ibid. 20.V.2018., N. Kuharić leg., CBSSC IT4398; 2 ♀♀, ibid., 20.V.2018, I. Jaklinović leg., CBSSC IT4251; 2 ♀♀, 1 juv., ibid., 20.V.2018, M. Čuček leg., CBSSC IT4399; 2 ♂♂, 1 ♂ juv., 2 ♀♀, Croatia, Starigrad Paklenica, Špecina špajza (cave), 44°17.10'N, 15°27.46'E, 29.VI.2013, A. Komerički leg., CBSSC IT3960; 2 ♀♀, ibid. 29.VI.2013, T. Dražina leg., CBSSC IT3961; 1 ♂, 1 ♀, ibid., 29.VI.2013, T. Dražina leg., CBSSC IT3962.

Type locality. Markova špilja, Seline, Starigrad Paklenica, Croatia (cave) (Bedek et al. 2019a).

Remarks. *Alpioniscus busljetai* n. sp. differs from Dinaric *Illyrionethes* species by the shallow and long rounded tergal hump of the male pereopod 7 carpus, similar to the one present only in *A. trogirensis* and *A. verhoeffi* Biokovo population. It differs from *A. trogirensis* in the shape of the male pleopod 1 exopod, with broadly rounded posterior apex and slightly concave outer margin (narrowly rounded posterior apex and sinuous outer margin in *A. trogirensis*). From A. verhoeffi it differs in more narrow apex and more wide basal part of pleopod 1 exopod. The shape of the male pleopod 1 exopod is similar to the one of *A. tuberculatus* (Frankenberger, 1939), from which it differs by the presence of the dorsal hump of the male pereopod 7 carpus and smooth habitus.

Distribution. The northern Dalmatia, Starigrad Paklenica area (Figure A. 19).

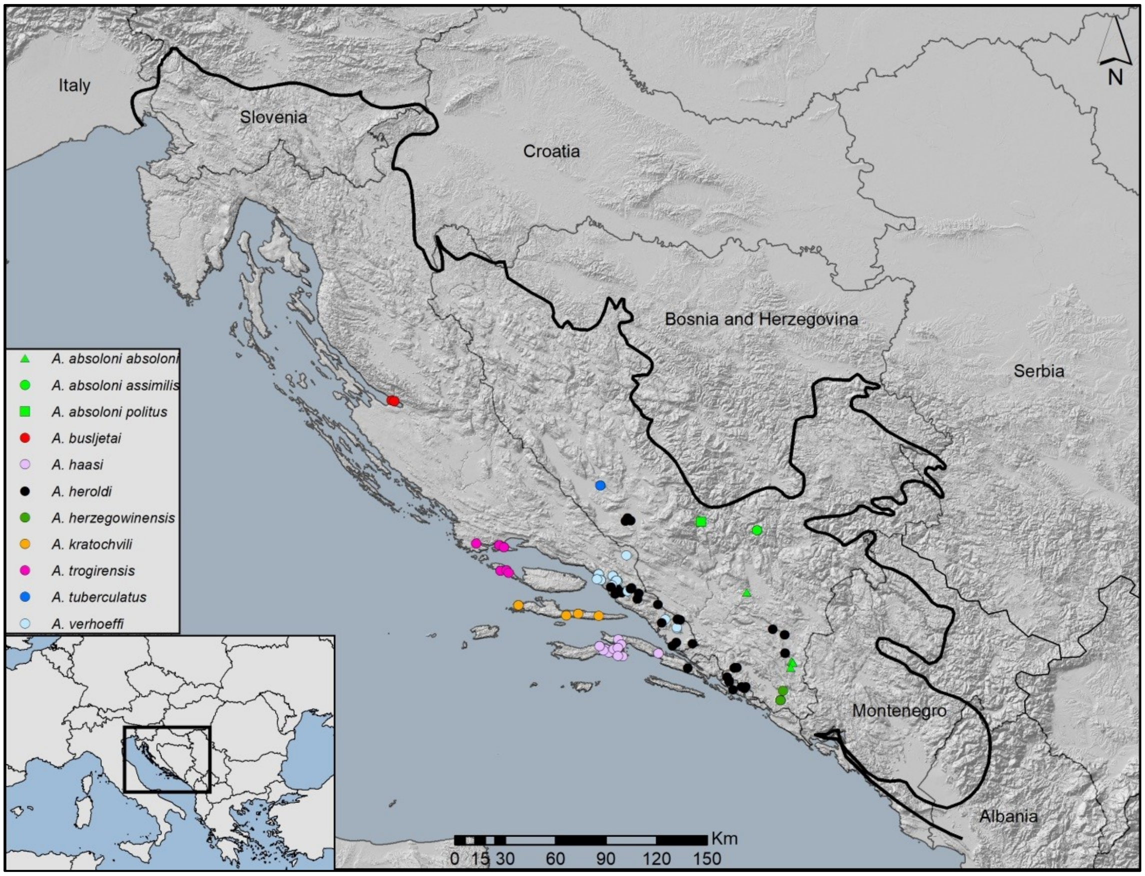


Figure A. 19. Distribution map of analysed specimens of the *Alpioniscus* species, *heroldi*-lineage in Dinaric Karst.

Appendix B. Morphometry analyses of the *Alpioniscus* (*Illyrionethes*) species, *strasseri*-lineage

The morphometric analyses were performed on the *strasseri*-lineage since it was thoroughly sampled and phylogenetically well-supported lineage. The analyses were carried out on the male dataset to identify and clarify new differential characters and to distinguish similar species with better precision. Besides body size and sexually dimorphic characters of 7th pereopod and 1st and 2nd pleopods, no sexual dimorphism is observed within previous taxonomic *Illyrionethes* analyses (e.g. Buturović 1957; Bedek and Taiti 2011; Horvatović 2014; Taiti et al. 2018), not unusual within Oniscidea (Lefebvre et al. 2000). The analyses of non-sexual characters were performed on males alone, to test if some of them could be used as differential or diagnostic characters. Since the high variability of non-sexual characters was observed in male specimens, and no species differential characters were recorded, females were not further analysed.

The phylogroups representing different taxonomic taxa and their subclades defined by Bedek et al. (2019c) were considered as the operational taxonomic units (OTUs). Nine OTUs (Northern and Southern Istria clades of *A. strasseri*, *A. christiani*, Cetina–Krka and Biokovo–Mosor clades of *A. balthasari*, Lika and Paklenica clades of *A. iapodicus*, *A. hirci* and *A. velebiticus*) were defined in this study (Table B 1). A subset of the largest males with fully developed secondary sexual characteristics were dissected out of total of 181 males collected from 102 different localities. The following appendages were dissected: antennulae, antennae, pereopods 1 and 7, genital papilla and pleopods 1 and 2. The dissected body parts were mounted on micropreparations, in Hoyer's liquid (Anderson, 1954). Body parts in micropreparations were photographed using Zeiss Primo Star, Canon EOS 40D and EOS Utility software and measured from photographs using AxioVision LE Software. Body size was measured under Zeiss Stemi 2000-C.

All together 31 characters were measured, four counted and three analysed descriptively (Table B 2). Body size was disregarded due to unreliability, and used only in species descriptions/redescriptions. Because of observed differences in body size between species and populations (Table C 1), i.e OTUs, the ratios are considered adequate for the elimination of the size influence, therefore statistically analysed (Table B 2).

Descriptive statistics (standard error, standard deviation, maximum, and minimum) measurements were recorded for each OTU, presented in Box-Whiskers plots. For each variable, average values were compared between different OTU by Kruskal–Wallis tests for the meristic parameters and ANOVA Welch test for the ratios parameters, followed by post hoc tests, Dunn's test and Tukey Unequal N HSD test, respectively (Zar 1999). These analyses were used to identify characters that express variability between OTUs. All statistical analyses were performed using STATISTICA software (release 13.3, StatSoft, 2019), and Microsoft Excel.

Table B 1. A list of operational taxonomic units (OTUs) analysed in the strasseri-lineage.

Species	subclade/locality	OTU abbreviations
Alpioniscus (*I.*) *strasseri*	Northern Istria	sN
Alpioniscus (*I.*) *strasseri*	Southern Istria	sS
Alpioniscus (*I.*) *christiani*	Croatian Litoral	c
Alpioniscus (*I.*) *balthasari*	Cetina–Krka	bCK
Alpioniscus (*I.*) *balthasari*	Biokovo–Mosor	bBM
Alpioniscus (*I.*) *iapodicus*	Lika	iL
Alpioniscus (*I.*) *iapodicus*	Paklenica	iP
Alpioniscus (*I.*) *hirci*	Gorski Kotar	h
Alpioniscus (*I.*) *velebiticus*	Velebit	v

Table B 2. A list of morphometric (M), numerical counted (N) and descriptive (D) characters including ratios (R) analysed in the strasseri-lineage.

Body part	Character	Data type	Morphometric character abbreviations
Antennula	Number of aestetascs	N	Anae
	1st article length	M	An1l
	2nd article lenght	M	An2l
	3rd article lenght	M	An3l
	1st/2nd articles lengths	R	An1l/An2l
	3rd/2nd articles lengths	R	An3l/An2l
	3rd/1st articles lengths	R	An3l/An1l
Antenna	Number of flagellum articles	N	Afar
	Number of flagellum articles bearing aestetascs	N	Afae
	Flagellum length	M	Afl
	5th article lengt	M	A5l
	5 th article width	M	A5w
	4 th article length	M	A4l
	4 th article width	M	A4w
	3 th article length	M	A3l
	3 th article width	M	A3w
	2 th article length	M	A2l
	2 th article width	M	A2w

Continuation of **Table B 2.**

Body part	Character	Data type	Morphometric character abbreviations
Antenna	2–5 th article + flagellum lengths	M	A2l+A3l+A4l+A5l+Afl
	Flagellum/5 th article length	R	Afl/A5l
	5 th article lenght/width	R	A5l/A5w
	2–5 th article + flagellum lengths /5 th article width	R	(A2l+A3l+A4l+A5l+Afl)/A5w
Pereopod	Protopodus 1 setae	N	P1s
	Merus lobe shape	D	Mlsh
	Merus lobe ditrection	D	Mldi
	Merus lobe size	D	Mlsi
	Carpus 7 length	M	C7l
	Carpus 7 width	M	C7w
	Carpus 7 hump length	M	C7hl
	Carpus 7 hump ending	M	C7he
	Carpus 7 hump height	M	C7hh
	Carpus 7 hump top position	M	C7ht
	Carpus 7 length/hump top position	R	C7l/C7ht
	Carpus 7 length/width	R	C7l/C7w
	Carpus 7 length/hump ending position	R	C7l/C7he
	Carpus 7 length/hump height	R	C7l/C7hh
	Carpus 7 hump length/height	R	C7hl/C7hh
Genital papilla	Length	M	GPl
	Width	M	GPw
	tip width	M	GPTw
	length/width	R	GPl/GPw
	width/tip width	R	GPw/GPTw
Pleopods	Exopod 1 length	M	Ex1l
	Exopod 1 width	M	Ex1w
	Exopod 1 tip width	M	Ex1tw
	exopod 1 turning point	M	Ex1tp
	Exopod 1 /genital papilla tip widths	R	Ex1tw/GPTw
	Exopod 1 tip width/ genital papilla width	R	Ex1tw/GPw
	Exopod 1 / genital papilla lenghts	R	Ex1l/GPl
	Exopod 1 length/turning point	R	Ex1l/Ex1tp
	Exopod 1 length/width	R	Ex1l/Ex1w
	Exopod 1 length/tip width	R	Ex1l/Ex1tw
	Exopod 1 width/tip width	R	Ex1w/Ex1tw
	Endopod 1 length	M	En1l
	Endopod 1 apical seta length	M	En1al
	Endopod 1 length/apical seta length	R	En1l/En1al

Continuation of **Table B 2.**

Body part	Character	Data type	Morphometric character abbreviations
Pleopods	Exopod 1/Endopod 1 length	R	Ex1l/En1l
	Endopod 2 article 1 length	M	En2a1l
	Endopod 2 article 1 length	M	En2a1l
	Endopod 2 article 2 with seta length	M	En2a2Sl
	Endopod 2 article 2 without seta length	M	En2a2l
	Endopod 2 article length 1/2 with seta	R	En2a1l/En2a2Sl
	Endopod 2 article length 1/2 without seta	R	En2a1l/En2a2l

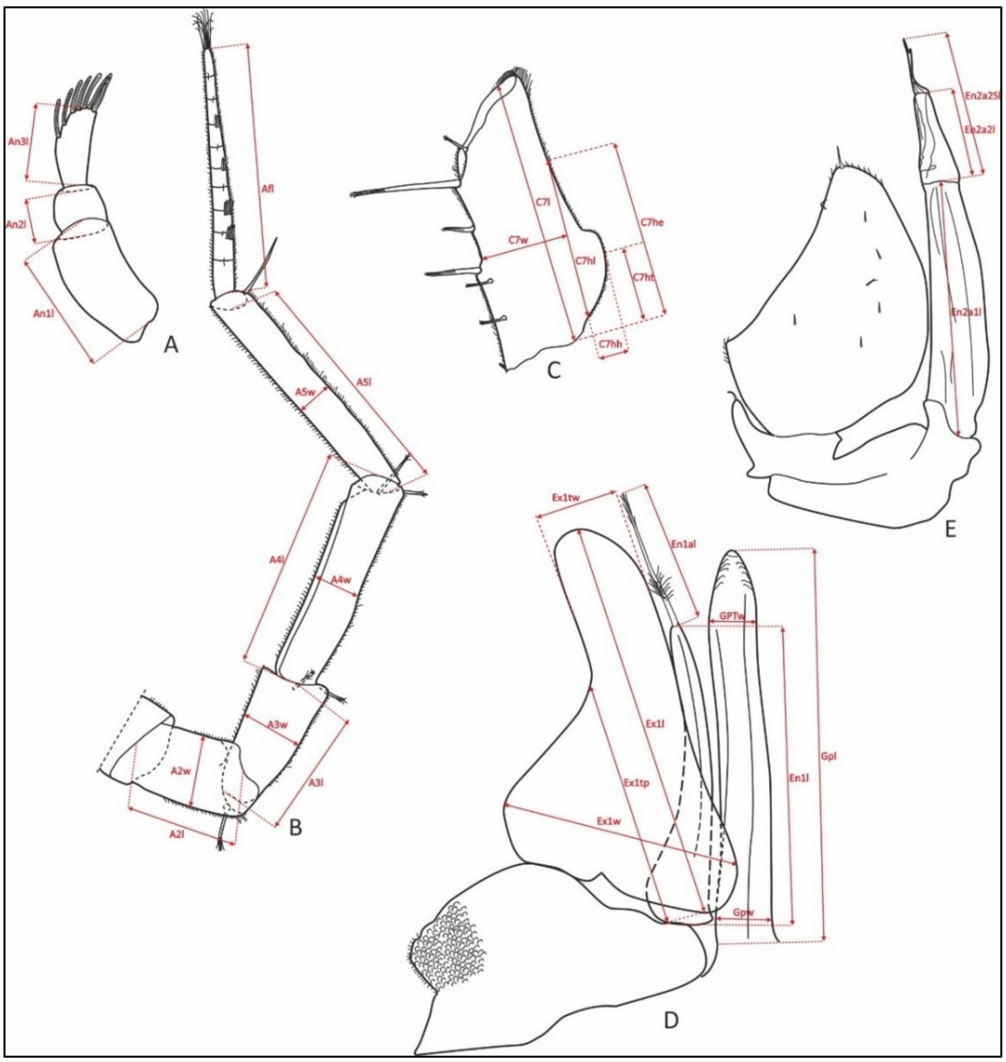


Figure B 1. Measurements: A, antennula; B, antenna, C, the male carpus of pereopod 7; D, the male genital papilla and pleopod 1; E, the male pleopod 2. The abbreviations characters are as in Table B 2.

Table B 3. Results of Kruskal-Wallis ANOVA tests for meristic characters analysed in *strasseri*-lineage. The values with statistically significant differences at p<0.05 are marked red. The abbreviations of characters are as in Table B 2 and fig. B 1.

Character	DF/N	H statistic	p
Afar	8/225	77.66421	< 0.00001
Afae	8/225	55.87875	< 0.00001
Anae	8/212	142.0295	< 0.0001
P1s	8/211	120.3437	< 0.0001

Table B 4. Dunn's test for significantly different characters according to Kruskal-Wallis ANOVA tests (Table B 3) analysed in *strasseri*-lineage. The values with statistically significant differences at p<0.05 are marked red. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and fig. B 1.

Depend.: Afar	bBM R:126,97	bCK R:136,32	c R:55,500	h R:116,13	iL R:98,071	iP R:154,13	sN R:129,46	sS R:103,93	v R:20,500
bBM		0,790834	2,558198	0,524718	1,488501	1,313226	0,124346	1,386832	6,818486
bCK	0,790834		2,909660	0,987169	1,993954	0,870766	0,346546	1,982122	7,559913
c	2,558198	2,909660		1,862631	1,340257	3,030136	2,302086	1,607127	1,182709
h	0,524718	0,987169	1,862631		0,704979	1,429896	0,511777	0,517751	4,182889
iL	1,488501	1,993954	1,340257	0,704979		2,188852	1,251964	0,260778	3,569839
iP	1,313226	0,870766	3,030136	1,429896	2,188852		0,946436	2,130891	5,845109
sN	0,124346	0,346546	2,302086	0,511777	1,251964	0,946436		1,111446	4,895175
sS	1,386832	1,982122	1,607127	0,517751	0,260778	2,130891	1,111446		4,329729
v	6,818486	7,559913	1,182709	4,182889	3,569839	5,845109	4,895175	4,329729	

Depend.: Afae	bBM R:123,97	bCK R:142,26	c R:39,917	h R:141,17	iL R:78,286	iP R:139,17	sN R:65,885	sS R:72,786	v R:81,080
bBM		1,548182	3,008582	0,831572	2,352986	0,734838	2,903352	3,080440	2,746876
bCK	1,548182		3,684804	0,053532	3,335556	0,151318	3,861787	4,252026	3,993659
c	3,008582	3,684804		3,110786	1,207955	3,049339	0,808264	1,090776	1,390979
h	0,831572	0,053532	3,110786		2,455456	0,075258	2,888876	2,902843	2,628349
iL	2,352986	3,335556	1,207955	2,455456		2,377358	0,494606	0,244877	0,128593
iP	0,734838	0,151318	3,049339	0,075258	2,377358		2,812128	2,817941	2,540864
sN	2,903352	3,861787	0,808264	2,888876	0,494606	2,812128		0,300404	0,682664
sS	3,080440	4,252026	1,090776	2,902843	0,244877	2,817941	0,300404		0,430452
v	2,746876	3,993659	1,390979	2,628349	0,128593	2,540864	0,682664	0,430452	

Depend.: Anae	bBM R:175,81	bCK R:80,718	c R:77,250	h R:94,400	iL R:93,600	iP R:158,45	sN R:88,000	sS R:94,132	v R:26,962
bBM		8,201101	3,743374	3,870747	4,618050	0,825293	4,798819	5,026108	10,25306
bCK	8,20110		0,131500	0,648786	0,720922	3,686009	0,396546	0,821701	3,68206
c	3,74337	0,131500		0,541393	0,551775	2,563330	0,359142	0,587663	1,81004
h	3,87075	0,648786	0,541393		0,031945	2,334732	0,251983	0,011200	2,95445
iL	4,61805	0,720922	0,551775	0,031945		2,589515	0,245658	0,025089	3,35041
iP	0,82529	3,686009	2,563330	2,334732	2,589515		2,773782	2,683775	5,76044
sN	4,79882	0,396546	0,359142	0,251983	0,245658	2,773782		0,283785	3,00163
sS	5,02611	0,821701	0,587663	0,011200	0,025089	2,683775	0,283785		3,62799
v	10,25306	3,682057	1,810042	2,954445	3,350412	5,760444	3,001630	3,627987	

Continuation of **Table B 4.**

Depend.: P1s	bBM R:162,13	bCK R:84,067	c R:61,600	h R:103,14	iL R:121,63	iP R:121,82	sN R:132,57	sS R:106,53	v R:20,440
bBM		6,747906	3,516453	2,911237	2,262857	1,989242	1,607627	3,329841	9,535241
bCK	6,747906		0,790540	0,952287	2,131448	1,885205	2,676638	1,368918	4,377809
c	3,516453	0,790540		1,261337	1,904099	1,828649	2,231193	1,455639	1,376104
h	2,911237	0,952287	1,261337		0,763198	0,717599	1,196566	0,145143	3,743544
iL	2,262857	2,131448	1,904099	0,763198		0,007627	0,482096	0,707690	5,074801
iP	1,989242	1,885205	1,828649	0,717599	0,007627		0,437131	0,654386	4,589243
sN	1,607627	2,676638	2,231193	1,196566	0,482096	0,437131		1,197040	5,501873
sS	3,329841	1,368918	1,455639	0,145143	0,707690	0,654386	1,197040		4,561367
v	9,535241	4,377809	1,376104	3,743544	5,074801	4,589243	5,501873	4,561367	

Table B 5. The normality tests of ratios analysed in *strasseri*-lineage. The values with statistically significant differences at p<0.05 are marked red. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and fig. B 1.

Character	Kolmogorov-Smirnov Test	Lilliefors Test	Shapiro-Wilk W Test
Afl/A5l	d=,05258, p> .20	p<,15	W=,99407, p=,51749
A5l/A5w	d=,03344, p> .20	p> .20	W=,99265, p=,31352
(A2l+A3l+A4l+A5l+Afl)/A5w	d=,09473, p<,05	p<,01	W=,97617, p=,00070
An1l/An2l	d=,11088, p<,05	p<,01	W=,97212, p=,00052
An3l/An2l	d=,10069, p<,05	p<,01	W=,97460, p=,00109
An3l/An1l	d=,09326, p<,10	p<,01	W=,98033, p=,00664
C7l/C7ht	d=,14896, p<,01	p<,01	W=,89286, p=,00000
C7l/C7w	d=,04460, p> .20	p> .20	W=,98873, p=,04
C7l/C7he	d=,12232, p<,01	p<,01	W=,91470, p=,00000
C7l/C7hh	d=,06369, p> .20	p<,05	W=,93036, p=,00000
C7hl/C7hh	d=,10642, p<,01	p<,01	W=,91938, p=,00000
GPl/GPw	d=,08911, p<,10	p<,01	W=,95433, p=,00000
GPw/GPTw	d=,06854, p> .20	p<,05	W=,98573, p=,03138
Ex1tw/GPTw	d=,09675, p<,05	p<,01	W=,97557, p=,00081
Ex1tw/GPw	d=,08129, p<,15	p<,01	W=,98157, p=,00733
Ex1l/GPl	d=,07543, p<,20	p<,01	W=,97022, p=,00027
Ex1l/Ex1tp	d=,07486, p<,15	p<,01	W=,96395, p=,00000
Ex1l/Ex1w	d=,06725, p<,20	p<,01	W=,97022, p=,00003
Ex1l/Ex1tw	d=,06411, p> .20	p<,05	W=,98632, p=,01519
Ex1w/Ex1tw	d=,04729, p> .20	p<,20	W=,98801, p=,03101
En1l/En1al	d=,09745, p<,05	p<,01	W=,93160, p=,00000
Ex1l/En1l	d=,04320, p> .20	p> .20	W=,98803, p=,04915
En2a1l/En2a2Sl	d=,07859, p<,10	p<,01	W=,97296, p=,00009
En2a1l/En2a2l	d=,06888, p<,20	p<,01	W=,98617, p=,01457

Table B 6. Results of ANOVA Welch tests for normally distributed ratio parameters according to Shapiro-Wilk WTest (Table B5), analysed in *strasseri*-lineage. The values with statistically significant differences at p<0.05 are marked red. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and fig. B 1.

Variable	SS Effect	df Effect	MS Effect	SS Error	df Error	MS Error	F	p	Welch df Effect	Welch df Error	Welch F	Welch p
(A2l+A3l+A4l+A5l+Afl)/A5w	1501,654	8	187,7067	2321,235	218	10,64787	17,62857	0,000000	8	47,76361	18,7410	0,000000
An1l/An2l	8,185	8	1,0231	17,402	191	0,09111	11,22984	0,000000	8	41,27364	14,2937	0,000000
An3l/An2l	3,512	8	0,4390	10,992	191	0,05755	7,62760	0,000000	8	40,67684	7,9279	0,000002
An3l/An1l	0,221	8	0,0276	1,449	191	0,00759	3,64159	0,000572	8	42,79546	3,4673	0,003641
C7l/C7ht	95,440	8	11,9300	33,784	228	0,14818	80,51232	0,000000	8	47,97241	124,3646	0,000000
C7l/C7w	8,686	8	1,0857	12,818	224	0,05722	18,97287	0,000000	8	50,18978	23,7397	0,000000
C7l/C7he	14,450	8	1,8063	4,615	228	0,02024	89,24205	0,000000	8	49,92002	95,1361	0,000000
C7l/C7hh	584,692	8	73,0865	1365,375	228	5,98849	12,20450	0,000000	8	48,65940	49,6147	0,000000
C7hl/C7hh	188,096	8	23,5120	360,813	228	1,58251	14,85741	0,000000	8	47,70241	21,4084	0,000000
GPl/GPw	56,383	8	7,0478	88,659	200	0,44329	15,89884	0,000000	8	35,47557	13,7116	0,000000
GPw/GPTw	12,471	8	1,5588	10,495	203	0,05170	30,15051	0,000000	8	34,28519	40,4898	0,000000
Ex1tw/GPTw	31,899	8	3,9873	18,907	208	0,09090	43,86584	0,000000	8	35,33881	40,4025	0,000000
Ex1tw/GPw	2,709	8	0,3386	4,862	202	0,02407	14,06782	0,000000	8	33,70005	11,4677	0,000000
Ex1l/GPl	0,784	8	0,0980	0,523	194	0,00269	36,36079	0,000000	8	32,62784	39,5854	0,000000
Ex1l/Ex1tp	10,609	8	1,3261	3,666	247	0,01484	89,35047	0,000000	8	66,33318	80,3781	0,000000
Ex1l/Ex1w	6,361	8	0,7952	4,312	247	0,01746	45,54559	0,000000	8	66,57959	38,5380	0,000000
Ex1l/Ex1tw	41,767	8	5,2209	28,434	247	0,11512	45,35256	0,000000	8	65,06178	49,7666	0,000000
Ex1w/Ex1tw	11,084	8	1,3855	9,055	248	0,03651	37,94645	0,000000	8	64,86528	44,3969	0,000000
En1l/En1al	7,822	8	0,9778	40,749	233	0,17489	5,59100	0,000002	8	59,49901	8,0340	0,000000
Ex1l/En1l	1,096	8	0,1370	1,038	221	0,00470	29,16163	0,000000	8	58,19811	44,7479	0,000000
En2a1l/En2a2Sl	13,178	8	1,6472	9,687	245	0,03954	41,66239	0,000000	8	61,00687	43,4856	0,000000
En2a1l/En2a2l	28,628	8	3,5785	28,780	246	0,11699	30,58792	0,000000	8	61,25089	31,5355	0,000000

Table B 7. Tukey Unequal N HSD post hoc test for significantly different characters according to ANOVA Welch tests of ratio parameters (Table B 6), analysed in *strasseri*-lineage. The values with statistically significant differences at $p<0.05$ are marked red. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and fig. B 1.

Error: Between MS = 9,7803, df = 121,00

(A2l+A3l+A4l+A5l+Afl)/A5w	bBM 29,740	bCK 28,489	c 23,350	h 24,414	iL 21,205	iP 28,829	sN 25,326	sS 27,797	v 25,056
bBM		0,777394	0,512844	0,009226	0,000010	0,999948	0,108753	0,813886	0,004272
bCK	0,777394		0,780814	0,126102	0,000036	1,000000	0,527435	0,999755	0,115655
c	0,512844	0,780814		0,999995	0,998967	0,713925	0,999432	0,889747	0,999810
h	0,009226	0,126102	0,999995		0,421204	0,384468	0,999685	0,345150	0,999966
iL	0,000010	0,000036	0,998967	0,421204		0,003711	0,171853	0,000294	0,181325
iP	0,999948	1,000000	0,713925	0,384468	0,003711		0,701636	0,999864	0,608526
sN	0,108753	0,527435	0,999432	0,999685	0,171853	0,701636		0,816112	1,000000
sS	0,813886	0,999755	0,889747	0,345150	0,000294	0,999864	0,816112		0,383228
v	0,004272	0,115655	0,999810	0,999966	0,181325	0,608526	1,000000	0,383228	

Error: Between MS = ,07758, df = 121,00

An1l/An2l	bBM 2,1360	bCK 2,1096	c 2,3000	h 2,1323	iL 2,1714	iP 1,7857	sN 2,1512	sS 2,0447	v 1,6615
bBM		0,999985	0,999663	1,000000	0,999999	0,551465	1,000000	0,995787	0,000499
bCK	0,999985		0,998991	1,000000	0,999938	0,656216	0,999998	0,999639	0,001370
c	0,999663	0,998991		0,999602	0,999947	0,650862	0,999838	0,992108	0,346485
h	1,000000	1,000000	0,999602		0,999998	0,566383	1,000000	0,999153	0,010167
iL	0,999999	0,999938	0,999947	0,999998		0,412380	1,000000	0,988867	0,003305
iP	0,551465	0,656216	0,650862	0,566383	0,412380		0,490779	0,869624	0,998734
sN	1,000000	0,999998	0,999838	1,000000	1,000000	0,490779		0,997738	0,013013
sS	0,995787	0,999639	0,992108	0,999153	0,988867	0,869624	0,997738		0,013427
v	0,000499	0,001370	0,346485	0,010167	0,003305	0,998734	0,013013	0,013427	

Error: Between MS = ,05272, df = 121,00

An3l/An2l	bBM 1,5193	bCK 1,5704	c 1,7000	h 1,7106	iL 1,6780	iP 1,3690	sN 1,5970	sS 1,4593	v 1,2773
bBM		0,992018	0,997234	0,703869	0,870997	0,982601	0,999057	0,999171	0,152361
bCK	0,992018		0,999755	0,933139	0,986505	0,903248	1,000000	0,949298	0,031234
c	0,997234	0,999755		1,000000	1,000000	0,881864	0,999957	0,981087	0,654615
h	0,703869	0,933139	1,000000		0,999998	0,311031	0,986962	0,329151	0,002055
iL	0,870997	0,986505	1,000000	0,999998		0,454109	0,998729	0,528850	0,006632
iP	0,982601	0,903248	0,881864	0,311031	0,454109		0,821393	0,999496	0,999432
sN	0,999057	1,000000	0,999957	0,986962	0,998729	0,821393		0,956908	0,119690
sS	0,999171	0,949298	0,981087	0,329151	0,528850	0,999496	0,956908		0,528199
v	0,152361	0,031234	0,654615	0,002055	0,006632	0,999432	0,119690	0,528199	

Error: Between MS = ,17243, df = 121,00

C7l/C7ht	bBM 2,6150	bCK 2,7367	c 3,0252	h 1,6432	iL 2,0629	iP 2,6152	sN 3,6896	sS 4,4010	v 2,1244
bBM		0,955054	0,987071	0,000033	0,109266	1,000000	0,000018	0,000010	0,064957
bCK	0,955054		0,998864	0,000011	0,016837	0,999946	0,000183	0,000010	0,005362
c	0,987071	0,998864		0,024642	0,331319	0,987115	0,805234	0,025871	0,425975
h	0,000033	0,000011	0,024642		0,443056	0,006662	0,000010	0,000010	0,252537
iL	0,109266	0,016837	0,331319	0,443056		0,471005	0,000010	0,000010	0,999997
iP	1,000000	0,999946	0,987115	0,006662	0,471005		0,001435	0,000010	0,635485
sN	0,000018	0,000183	0,805234	0,000010	0,000010	0,001435		0,017752	0,000010
sS	0,000010	0,000010	0,025871	0,000010	0,000010	0,000010	0,017752		0,000010
v	0,064957	0,005362	0,425975	0,252537	0,999997	0,635485	0,000010	0,000010	

Continuation of **Table B 7.**

Error: Between MS = ,05748, df = 121,00

C7l/C7w	bBM 3,0854	bCK 2,9733	c 2,5161	h 2,6789	iL 2,8062	iP 2,9098	sN 2,9346	sS 2,7287	v 2,6568
bBM		0,593495	0,297784	0,009763	0,246144	0,964924	0,943033	0,004698	0,000207
bCK	0,593495		0,608836	0,184417	0,865801	0,999975	0,999997	0,186042	0,021775
c	0,297784	0,608836		0,999037	0,954590	0,781404	0,718079	0,993686	0,999672
h	0,009763	0,184417	0,999037		0,970442	0,845205	0,450694	0,999963	1,000000
iL	0,246144	0,865801	0,954590	0,970442		0,998993	0,978319	0,998971	0,925126
iP	0,964924	0,999975	0,781404	0,845205	0,998993		1,000000	0,957954	0,765875
sN	0,943033	0,999997	0,718079	0,450694	0,978319	1,000000		0,736069	0,331434
sS	0,004698	0,186042	0,993686	0,999963	0,998971	0,957954	0,736069		0,997739
v	0,000207	0,021775	0,999672	1,000000	0,925126	0,765875	0,331434	0,997739	

Error: Between MS = ,01903, df = 121,00

C7l/C7he	bBM 1,5205	bCK 1,4307	c 1,7904	h 1,2713	iL 1,2753	iP 1,4182	sN 2,0618	sS 1,9183	v 1,1503
bBM		0,153907	0,574106	0,004051	0,005136	0,962272	0,000010	0,000010	0,000010
bCK	0,153907		0,183429	0,256015	0,289260	1,000000	0,000010	0,000010	0,000017
c	0,574106	0,183429		0,005283	0,005898	0,148324	0,565943	0,991491	0,000152
h	0,004051	0,256015	0,005283		1,000000	0,756890	0,000010	0,000010	0,640650
iL	0,005136	0,289260	0,005898	1,000000		0,784116	0,000010	0,000010	0,597634
iP	0,962272	1,000000	0,148324	0,756890	0,784116		0,000010	0,000011	0,054784
sN	0,000010	0,000010	0,565943	0,000010	0,000010	0,000010		0,485933	0,000010
sS	0,000010	0,000010	0,991491	0,000010	0,000010	0,000011	0,485933		0,000010
v	0,000010	0,000017	0,000152	0,640650	0,597634	0,054784	0,000010	0,000010	

Error: Between MS = 4,2032, df = 121,00

C7l/C7hh	bBM 10,303	bCK 10,166	c 11,583	h 6,6274	iL 10,326	iP 8,7246	sN 10,190	sS 9,5516	v 5,8766
bBM		0,999999	0,999481	0,004520	1,000000	0,952914	1,000000	0,991007	0,000011
bCK	0,999999		0,998903	0,007731	1,000000	0,972732	1,000000	0,997768	0,000013
c	0,999481	0,998903		0,274236	0,999545	0,900362	0,999031	0,986800	0,120130
h	0,004520	0,007731	0,274236		0,004126	0,795547	0,015035	0,062447	0,997479
iL	1,000000	1,000000	0,999545	0,004126		0,948837	1,000000	0,996860	0,000174
iP	0,952914	0,972732	0,900362	0,795547	0,948837		0,969838	0,999392	0,407872
sN	1,000000	1,000000	0,999031	0,015035	1,000000	0,969838		0,999493	0,000884
sS	0,991007	0,997768	0,986800	0,062447	0,996860	0,999392	0,999493		0,000198
v	0,000011	0,000013	0,120130	0,997479	0,000174	0,407872	0,000884	0,000198	

Error: Between MS = 1,2893, df = 121,00

C7hl/C7hh	bBM 5,9885	bCK 6,0728	c 5,1667	h 4,5907	iL 6,8111	iP 5,2230	sN 4,3374	sS 4,3718	v 4,5845
bBM		0,999998	0,998476	0,181647	0,838257	0,978964	0,086655	0,008663	0,042924
bCK	0,999998		0,996953	0,124645	0,905889	0,960172	0,057081	0,004253	0,023565
c	0,998476	0,996953		0,999890	0,878973	1,000000	0,998373	0,998801	0,999881
h	0,181647	0,124645	0,999890		0,001132	0,993992	0,999959	0,999979	1,000000
iL	0,838257	0,905889	0,878973	0,001132		0,398017	0,000471	0,000208	0,001078
iP	0,978964	0,960172	1,000000	0,993992	0,398017		0,949288	0,959775	0,993578
sN	0,086655	0,057081	0,998373	0,999959	0,000471	0,949288		1,000000	0,999966
sS	0,008663	0,004253	0,998801	0,999979	0,000208	0,959775	1,000000		0,999931
v	0,042924	0,023565	0,999881	1,000000	0,001078	0,993578	0,999966	0,999931	

Error: Between MS = ,52313, df = 121,00

GPl/GPw	bBM 4,5000	bCK 6,0323	c 4,8438	h 5,2063	iL 4,9382	iP 5,3039	sN 4,9834	sS 5,1151	v 4,7419
bBM		0,000010	0,999933	0,492916	0,935923	0,710429	0,920374	0,426682	0,995171
bCK	0,000010		0,780789	0,271427	0,036055	0,809365	0,088540	0,033429	0,000215
c	0,999933	0,780789		0,999900	1,000000	0,999403	1,000000	0,999989	1,000000
h	0,492916	0,271427	0,999900		0,997248	1,000000	0,999528	0,999999	0,911945
iL	0,935923	0,036055	1,000000	0,997248		0,996913	1,000000	0,999870	0,999716
iP	0,710429	0,809365	0,999403	1,000000	0,996913		0,998795	0,999977	0,950405
sN	0,920374	0,088540	1,000000	0,999528	1,000000	0,998795		0,999991	0,999148
sS	0,426682	0,033429	0,999989	0,999999	0,999870	0,999977	0,999991		0,927099
v	0,995171	0,000215	1,000000	0,911945	0,999716	0,950405	0,999148	0,927099	

Continuation of **Table B 7.**

Error: Between MS = ,04900, df = 121,00

GPw/GPTw	bBM 1,9443	bCK 2,0942	c 1,3427	h 1,3196	iL 1,5962	iP 1,6694	sN 2,0512	sS 1,9736	v 1,5751
bBM		0,117670	0,141232	0,000010	0,023963	0,568731	0,988849	0,999995	0,000729
bCK	0,117670		0,019722	0,000010	0,000071	0,060878	0,999986	0,902232	0,000010
c	0,141232	0,019722		1,000000	0,967234	0,866894	0,036953	0,101109	0,980874
h	0,000010	0,000010	1,000000		0,165777	0,232233	0,000010	0,000010	0,257604
iL	0,023963	0,000071	0,967234	0,165777		0,999862	0,001317	0,009083	1,000000
iP	0,568731	0,060878	0,866894	0,232233	0,999862		0,138089	0,423484	0,999091
sN	0,988849	0,999986	0,036953	0,000010	0,001317	0,138089		0,998783	0,000593
sS	0,999995	0,902232	0,101109	0,000010	0,009083	0,423484	0,998783		0,000183
v	0,000729	0,000010	0,980874	0,257604	1,000000	0,999091	0,000593	0,000183	

Error: Between MS = ,08496, df = 121,00

Ex1tw/GPTw	bBM 2,2581	bCK 2,9246	c 1,6329	h 1,8070	iL 2,1345	iP 2,3652	sN 2,0920	sS 2,4277	v 1,9058
bBM		0,000010	0,442368	0,028531	0,993074	0,999694	0,968255	0,863496	0,053184
bCK	0,000010		0,000345	0,000010	0,000011	0,060903	0,000011	0,000492	0,000010
c	0,442368	0,000345		0,999626	0,733652	0,225626	0,818539	0,138292	0,990900
h	0,028531	0,000010	0,999626		0,292710	0,061978	0,574500	0,000243	0,998540
iL	0,993074	0,000011	0,733652	0,292710		0,944828	0,999998	0,450069	0,768409
iP	0,999694	0,060903	0,225626	0,061978	0,944828		0,864205	0,999995	0,235601
sN	0,968255	0,000011	0,818539	0,574500	0,999998	0,864205		0,339915	0,938026
sS	0,863496	0,000492	0,138292	0,000243	0,450069	0,999995	0,339915		0,000202
v	0,053184	0,000010	0,990900	0,998540	0,768409	0,235601	0,938026	0,000202	

Error: Between MS = ,02419, df = 121,00

Ex1tw/GPw	bBM 1,1703	bCK 1,4048	c 1,2188	h 1,3762	iL 1,3445	iP 1,4285	sN 1,0365	sS 1,2324	v 1,2164
bBM		0,000010	0,999997	0,112865	0,296916	0,176224	0,734121	0,984259	0,997932
bCK	0,000010		0,957565	0,999985	0,996255	1,000000	0,000109	0,107878	0,051991
c	0,999997	0,957565		0,984870	0,996658	0,916610	0,962428	1,000000	1,000000
h	0,112865	0,999985	0,984870		0,999968	0,999844	0,000451	0,571080	0,419083
iL	0,296916	0,996255	0,996658	0,999968		0,995148	0,002436	0,842104	0,716568
iP	0,176224	1,000000	0,916610	0,999844	0,995148		0,002213	0,548220	0,434774
sN	0,734121	0,000109	0,962428	0,000451	0,002436	0,002213		0,222493	0,334087
sS	0,984259	0,107878	1,000000	0,571080	0,842104	0,548220	0,222493		0,999999
v	0,997932	0,051991	1,000000	0,419083	0,716568	0,434774	0,334087	0,999999	

Error: Between MS = ,00271, df = 121,00

Ex1l/GPl	bBM 1,0179	bCK 1,0715	c 1,1291	h ,95258	iL ,98496	iP ,95389	sN ,98250	sS ,97487	v 1,1816
bBM		0,000765	0,449257	0,163057	0,919430	0,584521	0,913531	0,470303	0,000010
bCK	0,000765		0,973526	0,000054	0,012757	0,010838	0,018452	0,000112	0,000012
c	0,449257	0,973526		0,020222	0,125413	0,021982	0,111265	0,075155	0,985221
h	0,163057	0,000054	0,020222		0,926206	1,000000	0,966668	0,992638	0,000010
iL	0,919430	0,012757	0,125413	0,926206		0,990471	1,000000	0,999978	0,000010
iP	0,584521	0,010838	0,021982	1,000000	0,990471		0,994529	0,999400	0,000010
sN	0,913531	0,018452	0,111265	0,966668	1,000000	0,994529		0,999998	0,000010
sS	0,470303	0,000112	0,075155	0,992638	0,999978	0,999400	0,999998		0,000010
v	0,000010	0,000012	0,985221	0,000010	0,000010	0,000010	0,000010	0,000010	

Error: Between MS = ,01642, df = 121,00

Ex1l/Ex1tp	bBM 1,6875	bCK 2,1965	c 2,0349	h 1,7720	iL 1,9556	iP 1,9405	sN 1,7063	sS 1,8996	v 2,2226
bBM		0,000010	0,143786	0,898484	0,000335	0,047178	0,999998	0,000838	0,000010
bCK	0,000010		0,942331	0,000010	0,002187	0,042016	0,000010	0,000010	0,999869
c	0,143786	0,942331		0,507223	0,999515	0,998267	0,201750	0,980211	0,871745
h	0,898484	0,000010	0,507223		0,060051	0,488393	0,983450	0,464934	0,000010
iL	0,000335	0,002187	0,999515	0,060051		1,000000	0,003204	0,991478	0,000363
iP	0,047178	0,042016	0,998267	0,488393	1,000000		0,091139	0,999896	0,014694
sN	0,999998	0,000010	0,201750	0,983450	0,003204	0,091139		0,063927	0,000010
sS	0,000838	0,000010	0,980211	0,464934	0,991478	0,999896	0,063927		0,000010
v	0,000010	0,999869	0,871745	0,000010	0,000363	0,014694	0,000010	0,000010	

Continuation of **Table B 7.**

Error: Between MS = ,01914, df = 121,00

Ex1l/Ex1w	bBM 1,6447	bCK 2,0686	c 1,8248	h 1,7783	iL 1,8564	iP 1,8416	sN 1,7522	sS 1,6602	v 1,9634
bBM		0,000010	0,931191	0,508964	0,032170	0,373166	0,829207	0,999999	0,000010
bCK	0,000010		0,707161	0,000319	0,031235	0,188523	0,000195	0,000010	0,586484
c	0,931191	0,707161		0,999995	1,000000	1,000000	0,999859	0,958902	0,985826
h	0,508964	0,000319	0,999995		0,957463	0,998489	0,999989	0,674952	0,104442
iL	0,032170	0,031235	1,000000	0,957463		1,000000	0,853687	0,065770	0,781875
iP	0,373166	0,188523	1,000000	0,998489	1,000000		0,984020	0,492184	0,901077
sN	0,829207	0,000195	0,999859	0,999989	0,853687	0,984020		0,922373	0,057799
sS	0,999999	0,000010	0,958902	0,674952	0,065770	0,492184	0,922373		0,000011
v	0,000010	0,586484	0,985826	0,104442	0,781875	0,901077	0,057799	0,000011	

Error: Between MS = ,12270, df = 121,00

Ex1l/Ex1tw	bBM 3,9102	bCK 4,6045	c 4,4882	h 3,5826	iL 3,6181	iP 3,5427	sN 4,7554	sS 4,0445	v 4,6177
bBM		0,000010	0,776850	0,554851	0,703097	0,771837	0,000057	0,987902	0,000019
bCK	0,000010		0,999996	0,000010	0,000010	0,000066	0,994815	0,001529	1,000000
c	0,776850	0,999996		0,192674	0,239710	0,147959	0,997783	0,940974	0,999990
h	0,554851	0,000010	0,192674		1,000000	1,000000	0,000010	0,116011	0,000010
iL	0,703097	0,000010	0,239710	1,000000		0,999995	0,000010	0,193939	0,000010
iP	0,771837	0,000066	0,147959	1,000000	0,999995		0,000012	0,363611	0,000051
sN	0,000057	0,994815	0,997783	0,000010	0,000010	0,000012		0,001638	0,997266
sS	0,987902	0,001529	0,940974	0,116011	0,193939	0,363611	0,001638		0,001024
v	0,000019	1,000000	0,999990	0,000010	0,000010	0,000051	0,997266	0,001024	

Error: Between MS = ,03662, df = 121,00

Ex1w/Ex1tw	bBM 2,3822	bCK 2,2337	c 2,4605	h 2,0178	iL 1,9459	iP 1,9250	sN 2,7260	sS 2,4412	v 2,3628
bBM		0,037330	0,999979	0,001772	0,000055	0,005000	0,009869	0,997243	0,999999
bCK	0,037330		0,959813	0,286967	0,038169	0,207803	0,000019	0,126131	0,734643
c	0,999979	0,959813		0,333584	0,151481	0,115657	0,902910	1,000000	0,999885
h	0,001772	0,286967	0,333584		0,996991	0,997707	0,000010	0,000125	0,004163
iL	0,000055	0,038169	0,151481	0,996991		1,000000	0,000010	0,000011	0,000163
iP	0,005000	0,207803	0,115657	0,997707	1,000000		0,000010	0,000693	0,009073
sN	0,009869	0,000019	0,902910	0,000010	0,000010	0,000010		0,071725	0,004647
sS	0,997243	0,126131	1,000000	0,000125	0,000011	0,000693	0,071725		0,981482
v	0,999999	0,734643	0,999885	0,004163	0,000163	0,009073	0,004647	0,981482	

Error: Between MS = ,00494, df = 121,00

Ex1l/En1l	bBM 1,3033	bCK 1,3419	c 1,4583	h 1,2233	iL 1,2045	iP 1,1532	sN 1,2586	sS 1,2045	v 1,3948
bBM		0,363796	0,402018	0,276301	0,071127	0,021126	0,939781	0,010335	0,025484
bCK	0,363796		0,773343	0,010429	0,001146	0,000760	0,300797	0,000031	0,601504
c	0,402018	0,773343		0,023466	0,009315	0,000507	0,103683	0,009317	0,992821
h	0,276301	0,010429	0,023466		0,999748	0,818234	0,985591	0,999749	0,000018
iL	0,071127	0,001146	0,009315	0,999748		0,965767	0,837457	1,000000	0,000011
iP	0,021126	0,000760	0,000507	0,818234	0,965767		0,300573	0,965749	0,000012
sN	0,939781	0,300797	0,103683	0,985591	0,837457	0,300573		0,837519	0,003441
sS	0,010335	0,000031	0,009317	0,999749	1,000000	0,965749	0,837519		0,000010
v	0,025484	0,601504	0,992821	0,000018	0,000011	0,000012	0,003441	0,000010	

Error: Between MS = ,04023, df = 121,00

En2a1l/En2a2Sl	bBM 2,1111	bCK 2,3905	c 2,0661	h 1,9078	iL 1,8941	iP 2,0270	sN 1,8470	sS 1,7168	v 2,2639
bBM		0,000011	1,000000	0,439129	0,345024	0,999196	0,172714	0,000028	0,583372
bCK	0,000011		0,795673	0,000021	0,000015	0,097207	0,000012	0,000010	0,800450
c	1,000000	0,795673		0,997178	0,994972	1,000000	0,975446	0,720476	0,987206
h	0,439129	0,000021	0,997178		1,000000	0,990688	0,999580	0,528849	0,005206
iL	0,345024	0,000015	0,994972	1,000000		0,981098	0,999939	0,630963	0,002961
iP	0,999196	0,097207	1,000000	0,990688	0,981098		0,890783	0,259125	0,636214
sN	0,172714	0,000012	0,975446	0,999580	0,999939	0,890783		0,932168	0,001087
sS	0,000028	0,000010	0,720476	0,528849	0,630963	0,259125	0,932168		0,000010
v	0,583372	0,800450	0,987206	0,005206	0,002961	0,636214	0,001087	0,000010	

Continuation of **Table B 7.**

Error: Between MS = ,12244, df = 121,00

En2a1l/En2a2l	bBM 3,2043	bCK 3,5644	c 2,9449	h 2,7951	iL 2,7986	iP 2,9489	sN 2,7538	sS 2,5496	v 3,2953
bBM		0,000762	0,998187	0,241145	0,251957	0,965688	0,197114	0,000098	0,999195
bCK	0,000762		0,701855	0,000140	0,000151	0,120867	0,000156	0,000010	0,571069
c	0,998187	0,701855		0,999970	0,999975	1,000000	0,999809	0,969866	0,985868
h	0,241145	0,000140	0,999970		1,000000	0,998862	1,000000	0,861320	0,061278
iL	0,251957	0,000151	0,999975	1,000000		0,999038	0,999999	0,851388	0,065141
iP	0,965688	0,120867	1,000000	0,998862	0,999038		0,993943	0,679328	0,823862
sN	0,197114	0,000156	0,999809	1,000000	0,999999	0,993943		0,963244	0,051045
sS	0,000098	0,000010	0,969866	0,861320	0,851388	0,679328	0,963244		0,000012
v	0,999195	0,571069	0,985868	0,061278	0,065141	0,823862	0,051045	0,000012	

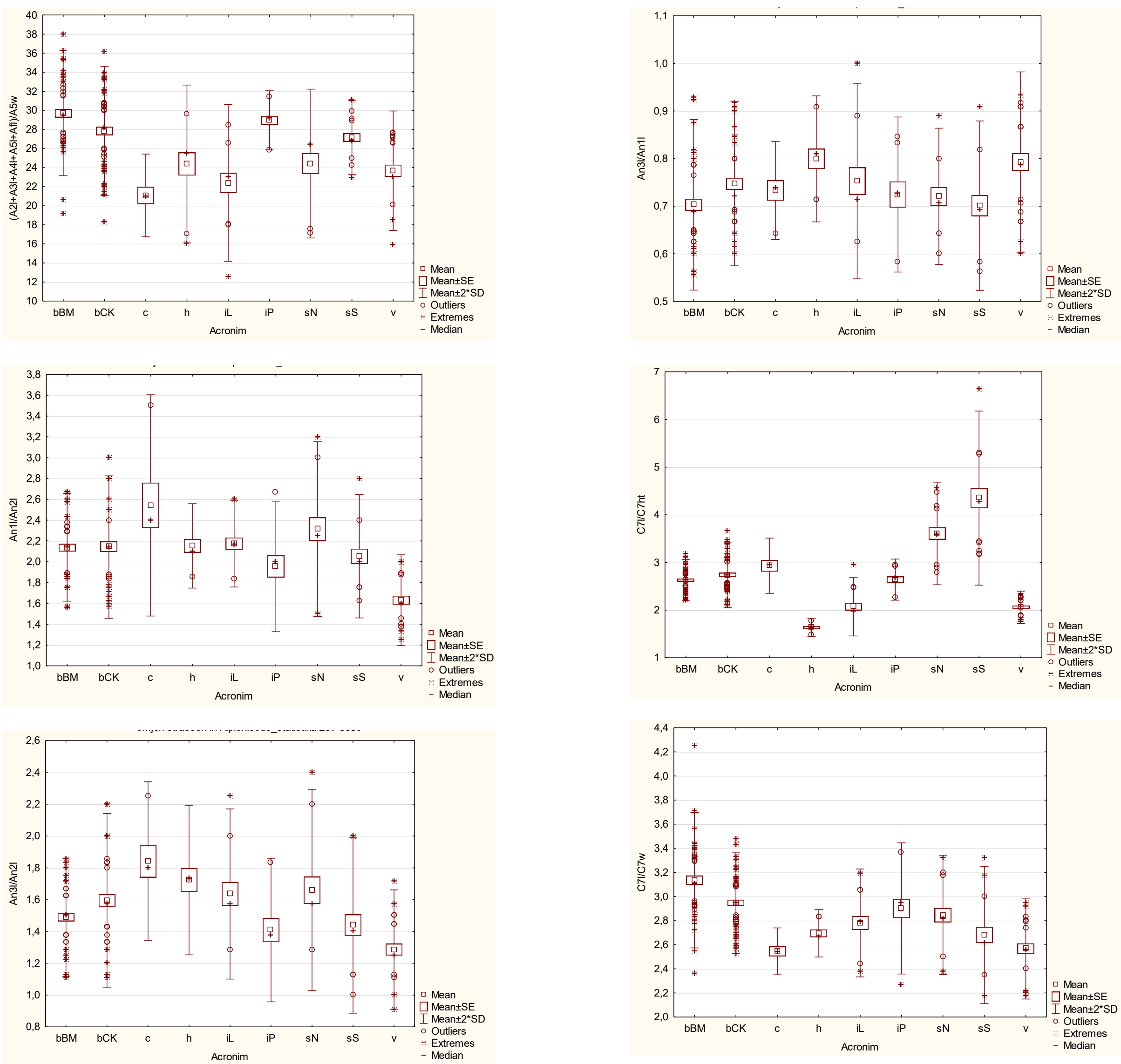
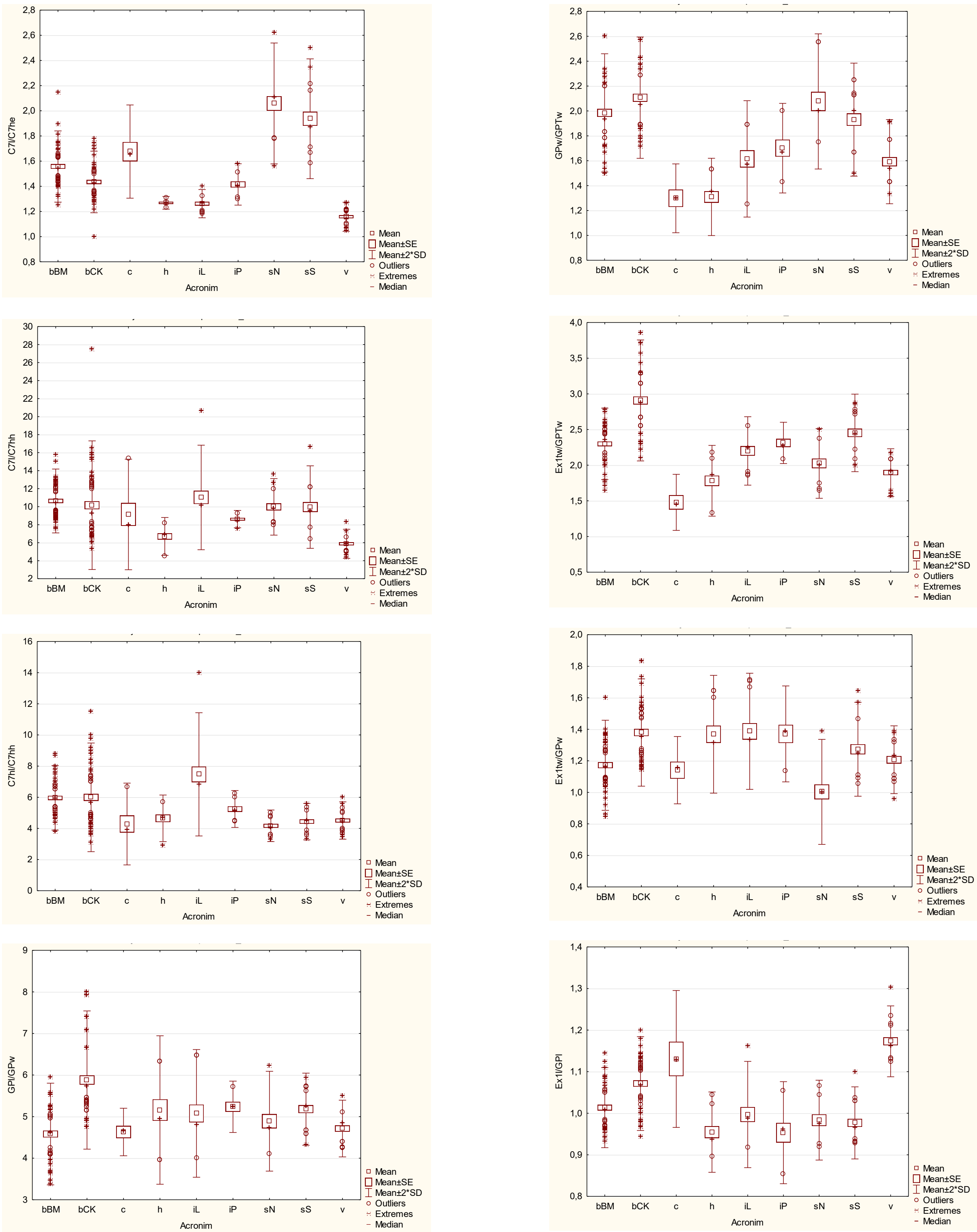
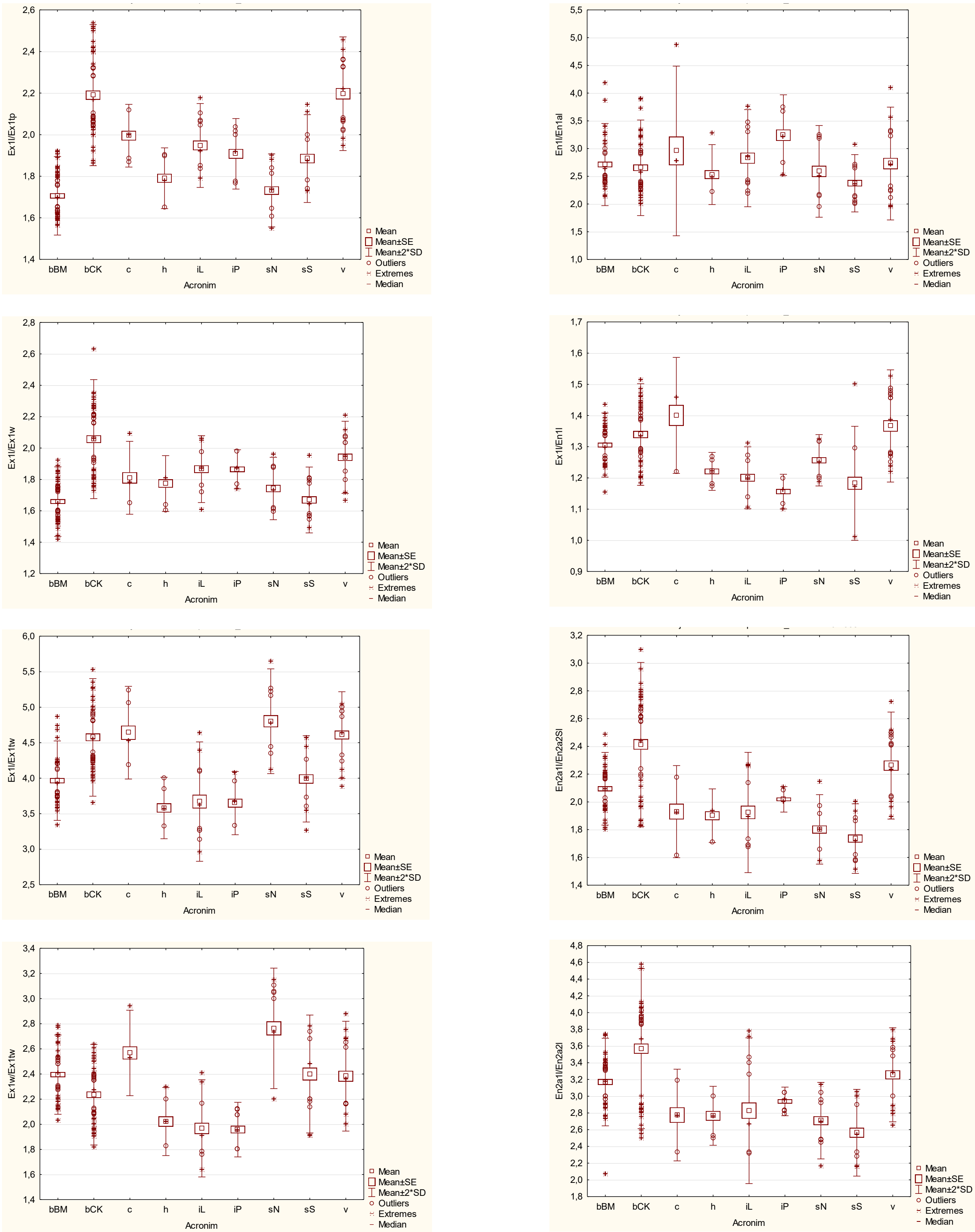


Figure B 2. The comparison of different ratio parameters analysed in *strasseri*-lineage. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and fig. B 1.



Continuation of **Figure B 2**.



Continuation of **Figure B 2.**

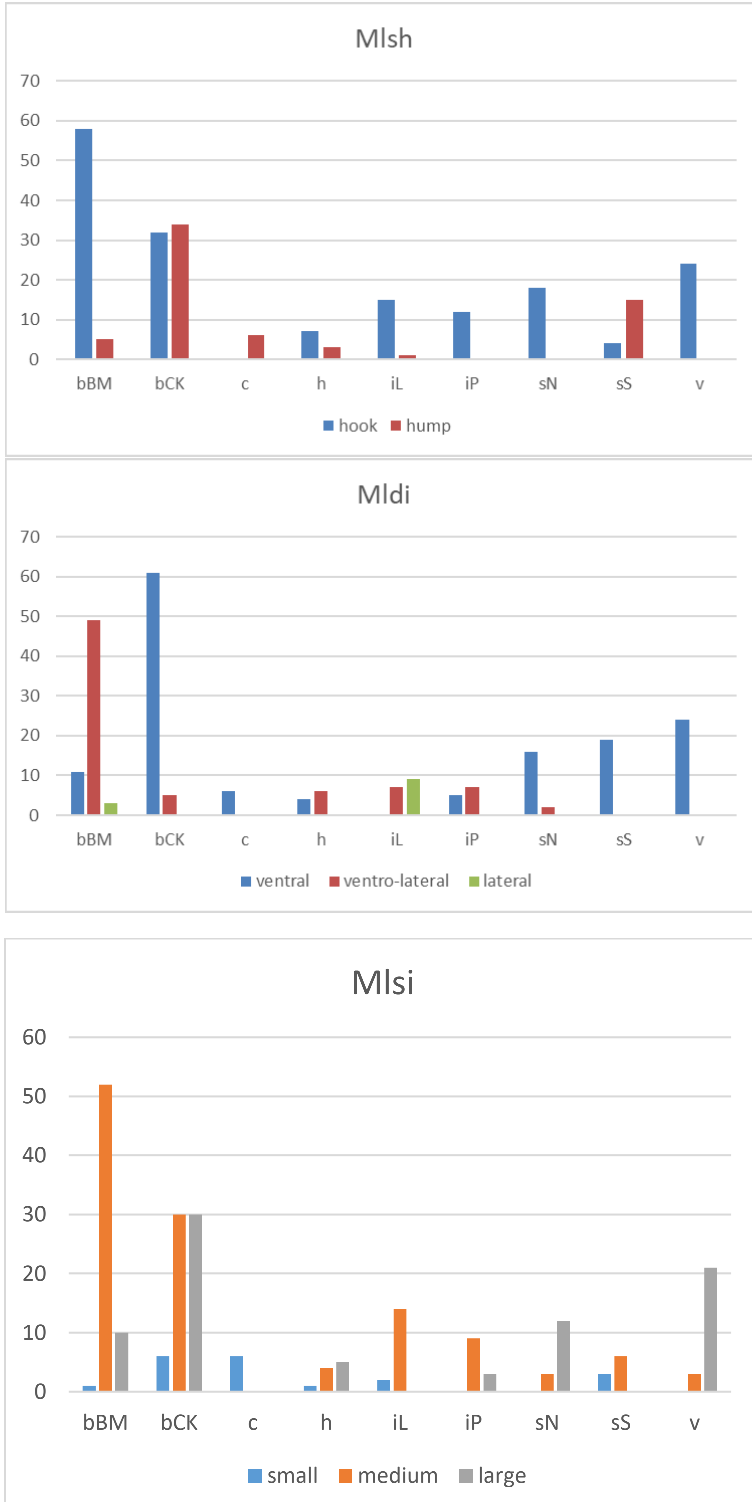


Figure B 3. The comparison of different descriptive characters in *strasseri*-lineage. The abbreviations of OTUs are as in Table B 1, characters are as in Table B 2 and Fig. B 1.

Appendix C. Differential characters of the Dinaric *Alpioniscus* (*Illyrionethes*) species

Table C 1. Habitus, antennula and antenna differential characters. The numbers of articles and aestetascs are expressed in range and mode.

lineage	species	subspecies/ population	habitus			antennula	antenna		
			length (♂; ♀/mm)	tegument	somites posterior margins ridges	no. aestetascs	peduncle	flagellum articles no.	flagellum articles with aestetascs no.
heroldi-lineage	*A. heroldi*		9.8; 10.2	smooth	no	6-11 8/10	smooth	7-10 9	4-6 4
	A. haasi		7.3; 8.4	smooth	no	7-10 7	smooth	9-11 10	4-6 4
	A. herzegowinensis		5.0; 7.2	smooth	cephalon, pereonites 1–3	7 7	granulated	8-9 8/9	3-4 4
	A. kratochvili		7.8; 8.6	smooth	no	7 7	smooth	9-10 9/10	4 4
	A. verhoeffi	Neretva	5.5; 6.1	smooth	cephalon, pereonites 1–3	9 9	granulated	6-8 6/8	3-4 3/4
		Biokovo	5.7; 7.5	granulated	cephalon, pereonites 1–6	8-13 13	granulated	8-10 8/10	4-6 4
	A. tuberculatus		4.5; 5.6	granulated	cephalon, pereonites, pleonites 1–3	6-7 7/6	granulated	7 7	4 4
	A. absoloni		5.2; 7.5	smooth/ granulated	cephalon, pereonites 1–5	6-9 7/9	granulated	6-8 7	3-4 4
	A. trogirensis		3.7; 5.5	granulated	cephalon, pereonites	6-7 6	granulated	5-7 6	2-3 3
	A. busljetai		4.4; 6.0	smooth	cephalon, pereonites	5-6 6	granulated	5-7 6	2-4 3
strasseri-lineage	*A. strasseri*	N Istria	5.8; 8.0	smooth	no	6-8 6/7	smooth	8-11 10	2-5 4
		S Istria	5.5; 7.5	smooth	no	6-9 7/8	smooth	8-10 10	2-5 4
	A. christiani		5.3; 8.0	smooth	no	4-8 7	smooth	7-9 8	2-4 3

Continuation of **Table C 1.**

Lineage	species	subspecies/ population	habitus			antennula	antenna		
			length (♂; ♀/mm)	tegument	somites posterior margins ridges	no. aestetascs	peduncle	flagellum articles no.	flagellum articles with aestetascs no.
strasseri-lineage	*A. balthasari*	Cetina–Krka	6.5; 7.8	smooth	cephalon, pereonites 1–4	4-7 7	smooth	8-13 10	2-7 5
		Biokovo–Mosor	7.5; 10.7	smooth	No	7-14 9	smooth	7-12 10	3-6 5
	A. iapodicus	Lika	6.9; 8.5	smooth	No	4-9 7	smooth	8-10 10	3-5 4
		Paklenica	6.5; 7.5	smooth	No	7-11 9	smooth	9-11 10	3-6 6
	A. hirci		6.7; 7.4	smooth	No	5-8 8	smooth	9-11 11	4-6 5
	A. velebiticus		6.5; 8.6	smooth	no	3-7 5	smooth	6-9 7	2-5 4
magnus-lineage	*A. magnus*		10.2; 11.2	smooth	no	5-11 8	smooth	8-12 10	3-6 5
	A. lossinii		4.9; 5.3	granulated	cephalon, pereonites, pleonites 1–2	5-7 5/6	granulated	8-10 8	4
	A. drazinai		5.2; 6.4	smooth	cephalon, pereonites 1–6	5-8 5	granulated	8-10 8	3-5 4
	A. mandalinae		3.5; 6.3	smooth - slightly granulated	cephalon, pereonites 1–6	6-8 8	granulated	7-10 8	3-5 4

Table C 2. Male pereopods differential characters. The number of setae is expressed in range and mode; the ratios are expressed in range and mean ± SD.

lineage	species	population	pereopod 1 carpus	pereopod 7 merus			pereopod 7 carpus				
			no. sternal setae	sternal lobe			hump			length/ hump top	length/ hump ending
				shape	size	direction	shape	position	distally protuberant		
heroldi-lineage	*A. heroldi*		5-6 6	hump	large	ventral	N/A	N/A	N/A	N/A	N/A
	A. haasi		6 6	hook	medium	ventro-lateral	N/A	N/A	N/A	N/A	N/A
	A. herzegowinensis		5-6 5	double hump	medium	ventral	N/A	N/A	N/A	N/A	N/A
	A. kratochvili		7 7	hook	medium	lateral	N/A	N/A	N/A	N/A	N/A
	A. verhoeffi	Neretva	5-6 6	hook	medium	N/A	N/A	N/A	N/A	N/A	N/A
		Biokovo	5-7 6	hook	medium	ventro-lateral	rounded	tergal	no	N/A	N/A
	A. tuberculatus		5 5	hook	medium	lateral	N/A	N/A	N/A	N/A	N/A
	A. absoloni		5 5	hook	large	ventral	rounded	tergal	no	N/A	N/A
	A. trogirensis		4-5 5	hook	small	lateral	rounded	tergal	no	N/A	N/A
	A. busljetai		4-6 5	hook	small	ventro-lateral	rounded	tergal	no	N/A	N/A
strasseri-lineage	*A. strasseri*	N Istria	6-7 6/7	hook	large	ventral	rounded	tergal	no	2.79–4.56 3.73±0.53	1.78–2.62 2.09±0.22
		S Istria	5-7 6	hump	small	ventral	rounded-pointed	tergal	no	3.17–6.64 4.42±0.97	1.58–2.21 1.88±0.19
	A. christiani		5-6 5/6	hump with teeth	small	ventral	rounded	tergal/ tergo-lateral	no	2.55–3.29 2.93±0.27	1.48–1.92 1.68±0.17

Continuation of **Table C 2.**

lineage	species	population	pereopod 1 carpus	pereopod 7 merus			pereopod 7 carpus				
			no. sternal setae	sternal lobe			hump			length/ hump top	length/ hump ending
				shape	size	direction	shape	position	distally protuberant		
strasseri-lineage	*A. balthasari*	Cetina–Krka	5-7 6	hook	medium	ventral	rounded	tergal	no	2.38–3.67 2.81±0.33	1.22–1.78 1.45±0.12
		Biokovo–Mosor	6-9 7	hook	medium	ventro-lateral	straight-rounded	tergal	no	2.21–3.18 2.65±0.22	1.25–2.15 1.57±0.15
	A. iapodicus	Lika	5-7 7	hook	small	lateral	straight-rounded	tergal/ tergo-lateral	no	1.81±2.95 2.10±0.36	1.20–1.31 1.23±0.03
		Paklenica	6-7 6	hook	medium	ventral	rounded	tergal	no	2.42–2.95 2.69±0.18	1.30–1.58 1.42±0.09
	A. hirci		6-7 6/7	hook	medium	ventral	straight-rounded	tergal	yes	1.49–1.77 1.66±0.09	1.23–1.31 1.27±0.03
	A. velebiticus		4-5 5	hook	large	ventral	rounded	tergal	no	1.80–2.33 2.08±0.15	1.05–1.27 1.16±0.06
magnus-lineage	*A. magnus*		5-7 6	hook	medium	ventral	straight	tergal	no	1.69±0.11	1.24±0.04
	A. lossinii		5-6 5	hook	small	ventral	N/A	N/A	N/A	N/A	N/A
	A. drazinai		5-7 6	hook	large	ventral	N/A	N/A	N/A	N/A	N/A
	A. mandalinae		5 5	hook	medium	ventral	N/A	N/A	N/A	N/A	N/A

Table C 3. Male pleopod 1 differential characters. The ratios are expressed in range, mean ± SD.

lineage	species	population	exopod					endopod
			outer margin	inner margin	apex	length/ apex width	length/ concavity turning point	basal part
heroldi-lineage	*A. heroldi*		slightly concave	straight	narrowly rounded	N/A	N/A	narrow
	A. haasi		sinuous	straight	narrowly rounded	N/A	N/A	narrow
	A. herzegowinensis		sinuous	straight	narrowly rounded	N/A	N/A	narrow
	A. kratochvili		slightly concave	straight	broadly rounded	N/A	N/A	narrow
	A. verhoeffi	Neretva	slightly concave	straight	broadly rounded	N/A	N/A	narrow
		Biokovo	almost straight-sinouos	straight	broadly rounded	N/A	N/A	narrow
	A. tuberculatus		slightly concave	slightly convex	broadly rounded	N/A	N/A	narrow
	A. absoloni		slightly concave	straight	narrowly rounded	N/A	N/A	narrow
	A. trogirensis		sinuous	straight	narrowly rounded	N/A	N/A	narrow
	A. busljetai		slightly concave	straight	broadly rounded	N/A	N/A	narrow
strasseri-lineage	*A. strasseri*	N Istria	deeply concave	slightly concave	narrowly rounded	4,12–5,65 4,76±0,38	1.61–1.88 1.73±0.07	narrow
		S Istria	deeply concave	slightly concave	narrowly rounded	3,60–4,57 4,07±0,31	1.78–2.14 1.90±0.09	narrow
	A. christiani		deeply concave	slightly concave	pointed to narrowly rounded	4,19–5,24 4,67±0,32	1.87–2.12 2.01±0.07	narrow
	A. balthasari	Cetina–Krka	deeply concave	straight to slightly concave	narrowly rounded	4,03–5,52 4,75±0,36	1.86–2.54 2.23±0.18	narrow
		Biokovo–Mosor	deeply concave	slightly concave	broadly rounded	3,34–4,86 3,97±0,28	1.56–1.92 1.70±0.10	narrow

Continuation of **Table C 3.**

lineage	species	population	exopod					endopod
			outer margin	inner margin	apex	length/ apex width	length/ concavity turning point	basal part
strasseri-lineage	*A. iapodicus*	Lika	deeply concave	straight to slightly concave	broadly rounded	3,14–4,64 3,68±0,52	1.79–2.07 1.93±0.10	narrow
		Paklenica	deeply concave	straight to slightly concave	medium rounded	3,33–4,08 3,68±0,22	1.77–2.04 1.91±0.09	narrow
	A. hirci		deeply concave	straight to slightly concave	broadly rounded	3,32–3,85 3,57±0,19	1.65–1.90 1.78±0.07	narrow
	A. velebiticus		deeply concave	straight to slightly concave	narrowly rounded	3,88–5,05 4,57±0,31	1.95–2.45 2.21±0.14	narrow
magnus-lineage	*A. magnus*		slightly sinuous	slightly sinuous	acute	N/A	N/A	wide
	A. lossinii		slightly concave	slightly convex	narrowly rounded	N/A	N/A	narrow
	A. drazinai		sinuous	slightly convex	broadly rounded	N/A	N/A	narrow
	A. mandalinae		almost straight	convex	narrowly rounded	N/A	N/A	wide

CURRICULUM VITAE

PERSONAL INFORMATION

- Name: Jana Bedek
- Birth date and place: 28. October 1976, Zagreb, Croatia

EDUCATION

- *1995. –2001***.** MSc in Biology – ecology, Faculty of Science, University of Zagreb

WORK EXPERIENCE

- *2017 –present* **Ministry of Environmental Protection and Energy** (former Croatian Agency for the Enviroment and Nature), Zagreb: Senior Expert Advisor for Caves and Karst
- *2017* **Antenula, obrt za poslovne usluge**, vl. Jana Bedek
- *2010 – 2015* **Croatian Biospeleological Society**, Zagreb: Professional Associate
- *2008 – 2009* **Croatian Biospeleological Society**, Zagreb: Professional Associate
- *2008* **DDD Ad libitum**, Zagreb: Associate Biologist
- *2006* **Croatian Natural History Museum**, Zagreb: Professional Associate
- *2003* **Croatian Natural History Museum**, Zagreb: Curator

MEMBERSHIPS

- *2006 – present* **International Society for Subterranean Biology SIBIOS/ISSB**
- *2001 – present* **Croatian Biospeleological Society**

AWARDS

- Whitley Award 2011
- Rufford Small Grant Booster Grant 2009
- Second Rufford Small Grant 2006
- Rufford Small Grant 2003

TYPE OF PUBLICATIONS (list in annex)

- Seven journal articles cited in the Web of Science core collection
- Seven peer-reviewed journal articles not cited in the Web of Science core collection
- Five books
- Seven book chapters
- One public database

CURRICULUM VITAE ANNEX: list of publications

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- **Bedek J,** Taiti S, Bilandžija H, Ristori E, Baratti M (2019) Molecular and taxonomic analyses in troglobiotic *Alpioniscus* (*Illyrionethes*) species from the Dinaric Karst (Isopoda: Trichoniscidae). Zoological Journal of the Linnean Society 187: 539–584. https://doi.org/10.1093/zoolinnean/zlz056
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