Invertebrate Fauna of the World

Volume 21, Number 2 Arthropoda: Crustacea: Harpacticoida: Parastenocarididae Parastenocaridid Copepods



Flora and Fauna of Korea

National Institute of Biological Resources Ministry of Environment



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2012

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Published by the National Institute of Biological Resources Environmental Research Complex, Nanji-ro 42, Seo-gu Incheon, 404-708, Republic of Korea www.nibr.go.kr

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ISBN : 9788997462001-96470 Government Publications Registration Number 11-1480592-000213-01

Printed by Junghaengsa, Inc. in Korea on acid-free paper

Publisher : Yeonsoon Ahn Project Staff : Joo-Lae Cho, Ye Eun, Sang-Hoon Hahn

Published on March 23, 2012



The Flora and Fauna of Korea logo was designed to represent six major target groups of the project including vertebrates, invertebrates, insects, algae, fungi, and bacteria. The book cover and the logo were designed by Jee-Yeon Koo.

Preface

Adoption of the 'Convention on Biological Diversity' in 1992 started to allow to acknowledge sovereign rights of the individual nations over biological and genetic resources, taking biological resources into considerations as one of the common properties of humankind. As such, it is one of the indicators for national competitiveness to create higher added-value of new variety, substance and medicine utilizing biological resources. In addition, adoption of the 'Nagoya protocol on access to genetic resources and the fair and equitable sharing of benefits arising from their utilization' in 2010 led to realization of international standards to fulfill biological sovereignty of the individual nations, which had lacked compulsory legal effect.

As it is expected that international competitions over biological resources will be stronger, national authorities on the globe have already begun to understand and organize the information of species inhabitant in their territories in order to prove their sovereignty over those biological resources; in this respect Korea seems to be outpaced by the advanced countries.

It is estimated that there are 100,000 or so of different species endemic to Korea among which about 38,000 species only are reported. Therefore, it is imperative to identify and organize indigenous biological resources known to date, as well as to strive continuously to discover new or unknown species. Indigenous species living in Korea can have such a significant influence on our lives that we must research them by and for ourselves.

Recognizing that it is the first priority to obtain and manage biological resources so as to secure the initiative of biotechnology industry in the future, National Institute of Biological Resources of the Ministry of Environment has been publishing Flora and Fauna of Korea for systematic and efficient management of biological resources of our own. For the last 4 years, professional research groups consisting of relevant professors and the like conducted systematic surveys and organizations for a variety of and wide range of taxa. As a result, 37 issues of Flora and Fauna of Korea, both in Korean and in English, covering 2,234 species and one issue of world monograph covering 173 species were published for the period of 2009 to 2011, and 28 issues of Flora and Fauna of Korea, both in Korean and in English, covering 1,475 species and one issue of world monograph covering 43 species are published this year.

I think, that these efforts to identify indigenous species living in Korea provide, not only the important evidences to claim sovereign rights over indigenous biological resources in Korea and to receive scientific certifications accordingly, but also provide the opportunity to prepare the framework for biotechnological industrialization of biological resources.

In conclusion, I would like to express sincere appreciation for those who did not spare their efforts to publish Biological Magazine and World Monograph; Professors I.H. Kim and H.S. Kim of Gangneung-Wonju National University, Professor K.T. Park of The Korean Academy of Science and Technology, Professor Y.J. Bae of Korea University, Dr. Y.S. Kwon of Korea National Park Service, Dr. T.H. Kang of National Academy of Agricultural Science, Dr. J.N. Kim of National Fisheries Research and Development Institute, Professor K.S. Lee of Dankook University, Professors J.G. Park and J.H. Lee of Daegu University, Professor S.W. Choi of Mokpo National University, Professor K.W. Nam of Pukyong National University, Professor S. Shin of Sahmyook University, Professor J.H. Lee of Sangmyung University, Professor S.T. Kim of Seoul National University, Emeritus Professor J.I. Kim of Sungshin Womens University, Professor J.H. Park of The University of Suwon, Professor H.S. Koh of Silla University, Professor J.E. Lee of Andong National University, Professor J.W. Lee and Dr. B.H. Jung of Yeungnam University, Professor M.K. Shin of Ulsan University, Dr. K.D. Han of Korea University, Professors D.H. Kwon and K.J. Cho of Inje University, Professor Y.S. Bae of University of Incheon, Professor J.Y. Park of Chonbuk National University, and Professor W.C. Lee and Dr. Tomislav Karanovic of Hanyang University.

Yeonsoon Ahn President NIBR

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List of Taxa

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Introduction

Parastenocarididae Chappuis, 1940 is a harpacticoid family highly specialised for life in continental groundwater, and its members are almost exclusively restricted to this habitat (Galassi and De Laurentiis 2004). They are, however, distributed on all continents except Antarctica and New Zealand (Karanovic 2004), remarkable considering that stygofauna has a limited active dispersal potential and lacks resting stages that could be dispersed passively (Culver and Pipan 2009). Because parastenocaridids have no marine relatives or modern pathways between different continents (Boxshall and Jaume 2000), it has been postulated that they have a Pangean origin (Karanovic 2006). In Australia, for example, Karanovic (2004) speculated that they started colonising subterranean waters just after the Permo-Carboniferous glaciation, which spread throughout much of what will subsequently become Gondwana supercontinent and covered the entire Australian plate (Frakes 1999; Playford 2003). This makes it likely that present distributions of most parastenocaridids are a result of continental drift (Boxshall and Jaume 2000), and thus an ideal group to study vicariance models in zoogeography. Unfortunately, no research has been done on their phylogeography so far, except for three genera from Australia (Karanovic and Cooper 2011a, b). Vicariance has been considered to be a more acceptable hypothesis for explaining zoogeographic connections of freshwater subterranean faunas with disjunct distribution patterns (Boxshall and Jaume 2000; Karanovic 2004, 2005a, 2006; Karanovic and Ranga Reddy 2005), whereas dispersal has been regarded traditionally as a better model for explaining recent disjunct distributions of marine and continental surface-water animals (Wilson 1999; Reid 2001; Waters and Roy 2004; Waters and Craw 2006; Karanovic 2008). This view was never challenged seriously, although recent debate about New Zealand biogeography showed that we have unjustly underestimated recent long-distance dispersal in favour of ancient vicariance (Sanmartin and Ronquist 2004; Waters and Craw 2006). Dispersal cannot be completely rejected even for some subterranean freshwater copepods with disjunct distributions (see Karanovic and Ranga Reddy 2004), although this can sometimes be a consequence of anthropogenic translocation associated with early shipping activities (Karanovic 2005b; Karanovic and Krajicek 2012). Research on families such as Parastenocarididae Chappuis, 1940 is thus very important to help resolve these complex zoogeographical issues. Unfortunately, so far most of the research effort was devoted to describing new species, which are scattered in numerous journals, sometimes very obscure, and presented in many languages. The original species descriptions for taxa presented in this monograph (and/or their redescriptons) were published in Chinese, Czech, English, French, German, Hungarian, Italian, Korean, Romanian, Russian, and Ukrainian (see the reference section below), on many occasions even without an English summary. Thus, a need to gather all these data has become apparent, as well as their critical treatment and reevaluation. This study offers the first insight into phylogenetic relationships of parastenocaridid copepods on a global scale, as well as redescriptions of species in English, and as many illustrations as deemed necessary for the present-day level of taxonomy in this group of copepods (or as many as available). We hope this will stimulate similar research on other groups of species, which will help us to understand better the evolution and historical zoogeography of this interesting and ancient group of subterranean copepods. This monograph is also intended to put the Korean Fauna into a more global perspective, and in this volume we treat the only two groups of parastenocaridids that occur in Korea, those from the proserpina and brevipes groups of species.

The family is a monophyletic group within Harpacticoida, being easily distinguished by the sexual dimorphism in the third pair of swimming legs (Corgosinho et al., 2007). Modification of these legs in males into a grasping organ, that allows them to hold females during copulation (Glatzel and Schminke 1996), is one of the most important synapomorphies of the group (Mertínez Arbizu and

Moura 1994), but many other morphological characters make it very easy to instantly recognize its members (Karanovic and Cooper 2011b). However, a great number of morphological characters are conservative within this family, making generic division a real and long lasting problem (Reid 1995; Galassi and De Laurentiis 2004; Karanovic 2005a; Schminke, 2010), and the family stayed monogeneric for a long time despite a steady accumulation of new species.

Chappuis (1937) divided its only genus *Parastenocaris* Kessler, 1913 into four groups, which he numbered rather than named, each containing two species. Kunz (1938) added another group. Lang (1948) subdivided the family into eight species groups for 31 of the 40 species known at that time (nine species were either known only as females or were insufficiently described), accepting the group proposed by Kunz (1938), but rearranging three of those proposed by Chappuis (1937) and naming them after the most characteristic species. For diagnosing all these groups all three authors mostly used characters of the male fourth leg endopod. Despite being chiefly based on a single character, Lang's system was widely accepted and was coping rather well with a subsequent steady influx of newly described species from around the world, culminating in the decade between 1963 and 1972 when 75 new species were added (Schminke, 2010). Five new species groups were added subsequently by Noodt (1962, 1963, 1972), mostly for the newly discovered and very diverse South American fauna, but it became apparent that this increasingly more complex system of species groups was not a reflection of true phylogenetic relationships, which were not taken into account in descriptions of many of newly proposed taxa (species and subsepcies).

Jakobi (1969) described one of the Noodt's groups as a new genus, and it was Jakobi (1972) who made the first effort to revise the family by splitting it into 26 different genera, although only assigning to them 98 out of the 155 then known species. This system was strongly criticised by Schminke (1976), and was ignored for a long time by most subsequent taxonomists working on this group, all of them accepting only two of Jakobi's genera (see Por and Hadel 1986; Dussart and Defaye 1990; Reid 1995; Karanovic and Bobic 1998; Ranga Reddy 2001; Galassi and De Laurentiis 2004; Boxshall and Halsey 2004; Karanovic 2005a, 2006; Cottarelli et al., 2006, 2007, 2008; Wells 2007; Ranga Reddy and Defaye 2007, 2009; Huys 2009). In a few isololated cases Jakobi's genera were treated as subgenera (see Kiefer 1976). Jakobi (1972), for example, divided the brevipes group of Lang (1948) into five different genera, which was shown by Reid (1995) to be a group of very closely related species. Reid (1995) even argued that the type species of one new genus proposed by Jakobi (Biwaecaris) is in fact a junior subjective synonym of the type species of *Parastenocaris*. Nevertheless, new genera were proposed for some unusual new members from South America (Dussart 1979; Reid 1994), Europe (Galassi and De Laurentiis 2004), Africa (Schminke 2009), Asia (Cottarelli et al., 2010), and Australia (Karanovic and Cooper 2011b), and two more groups of species were proposed by Berera and Cottarelli (2003) and Galassi and De Laurentiis (2004). Recently, some researchers (Corgosinho and Mertínez Arbizu 2005; Schminke 2008; Corgosinho et al., 2010; Karanovic et al., 2012) started to revalidate and redefine some genera originally proposed by Jakobi (1972), as most of them remained valid and available names under the rules of the ICZN (1999), while at the same time synonymizing some others.

The latest family revision was published by Schminke (2010), who listed all 258 species described until then in the family Parastenocarididae, provisionally accepted 27 genera as valid (accepting most of those described by Jakobi, although mainly listing just their type species as valid members), and subdivided the family into two subfamilies. As a result of the Principle of Coordination, Parastenocaridinae Chappuis, 1940 has already (potentially) existed since 1940, with *Parastenocaris* as its type genus. In that respect, "Parastenocaridinae nov.", Schminke's (2010) most frequent way to refer to the taxon, is an error. He does, however, correctly call it "Parastenocaridinae Chappuis, 1940" in three places in his paper. On the other hand, he seems reluctant to call these two groups subfamilies, putting the word "subfamily" in quotes in the abstract and noting that such subgroups as he is

proposing are "traditionally called subfamilies" (p. 344). Besides these instances, he does not use the term subfamily in the diagnosis section (pp. 361-362) or anywhere else. Still, the above quoted notation on p. 344, together with the frequent notation "nov.", is enough to show that he is intentionally proposing a new taxon (Fontinalicaridinae) of subfamily rank (i.e., it is not some sort of informal or "provisional" or Phylocode-type unavailable taxon), and he explicitly designates its type genus. Therefore, we think, he has (barely) met the requirements for availability of new names. Due mostly to incomplete descriptions or absence of males, he was able to classify only 112 species of Parastenocarididae to the genus level, leaving a majority of them in the genus *Parastenocaris*. Division of the genus *Parastenocaris* into *Parastenocaris s. str.* and *Parastenocaris s. l.*, as first proposed by Galassi and De Laurentiis (2004) and adopted with a different meaning by Schminke (2010), has neither nomenclatural bearing nor phylogenetic justification, as *sensu stricto* by definition must be part of *sensu lato*.

Karanovic et al. (2012) redefined recently the genus Proserpinicaris Jakobi, 1972 based on synapomorphic character states found in a group of 20 closely related species, including three new short range endemics from South Korea. Although technically this may be seen in stark contrast to Schimnke's (2010) monospecific concept of this genus, they actually built on his work and used many morphological characters recognised by him as phylogenetically informative. It was Kunz (1938) who first recognized that the Italian Parastenocaris proserpina Chappuis, 1938 is quite distant from the type species of the genus, and he proposed a separate group of species ("proserpina-Gruppe") for it and two other closely related congeners: the Spanish P. cantabrica Chappuis, 1937, and the German P. phyllura Kiefer, 1938; the latter species was subsequently found throughout central and northern Europe (see Enckel 1969). Lang (1948) acknowledged this group and added two more species: the Hungarian P. budapestensis Török, 1935, and the German P. nolli Kiefer, 1938. Although his action regarding P. budapestensis may be explained by a probable mix-up in Török's (1935) original drawings (see below), both species seem to be only remotely related to those included by Kunz (1938). Jakobi (1972) erected the genus Proserpinicaris for this group of species, with P. proserpina as its type species, recognised P. cantabrica, P. phyllura, and P. nolli as its valid members, and included two other species that were described post Lang (1948): the Czech P. moravica Šterba, 1965, and the Canadian P. delamarei Chappuis, 1958. He listed the publication date of the latter species erroneously as 1957, but *P. delamarei* was described in Chappuis and Delamare Debouteville (1958). Jakobi (1972) excluded P. budapestensis from this group and designated it the type species of his new genus Lacustricaris Jakobi, 1972, where he included additionally only the Canadian P. lacustris Chappuis, 1958 (also with the incorrect publication date of 1957). Amazingly, Schminke (2010) considered P. budapestensis as incertae sedis in Parastenocaridinae, while he listed Lacustricaris as a valid member of Fontinalicaridinae, and with L. lacustris (Chappuis, 1958) as its only member. This action is completely unjustified under the rules of the ICZN (1999), and may be a simple lapsus calami. We argue below that *P. budapestensis*, P. nolli, and P. delamarei are not at all closely related to the type species of Proserpinicaris, while P. cantabrica, P. phyllura, and P. moravica are.

Acknowledgements

Ms Renate Walter (Zoologisches Museum Hamburg, Germany) is kindly acknowledged for the help in preparation of the SEM photographs. Financial support to the senior author came from Brain Pool and NIBR grants (both in Korea), while the necessary facilities were provided by the Zoologisches Museum in Hamburg and Hanyang University in Seoul. We both want to thank Dr Joo-Lae Cho (National Institute of Biological Resources, Korea) for providing valuable material of Korean species. Dr Mark Grygier (Lake Biwa Museum, Japan) is acknowledged for his help in collecting material in Japan. Most data in this monograph are taken from literature, and usually from original descriptions. Type material of many species, unfortunately, is lost or inaccessible, often kept in private collections. All specimens of Korean species redescribed here were collected by staff of the National Institute of Biological Resources, Korea. Most of them were collected by the Karaman-Chappuis method, although some were also collected by various pumps from interstitial sediments. Specimens of the Japanese parastenocaridids were collected by the senior author also by the Karaman-Chappuis method. They were all fixed in 99% ethanol. Locality data and number of specimens are listed for each examined species separately, and all types and additionally examined specimens are deposited in the National Institute of Biological Resources (NIBR).

Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock and von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination water slowly evaporates and appendages eventually remained in a completely dry Faure's medium, ready for long term depositing. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, with N-PLAN (5x, 10x, 20x, 40x and 63x dry) or PL FLUOTAR (100x oil) objectives. Specimens that were not drawn were examined in propylene glycol (CH₃CH(OH)CH₂OH) and, after examination, were again preserved in 99.9% ethanol. Specimens for the scanning electron micrography were dehydrated in progressive ethanol concentrations, critical-point dried, coated in gold and observed under a LEO 1525 microscope on the in-lens detector, with working distances between 5.9 and 6.1 mm and accelerating voltages of 5 or 10 kV.

Morphological terminology follows Huys and Boxshall (1991), except for the caudal ramus setae numbering and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Biospeleological terminology follows Humphreys (2000). Taxa, from subfamilies to species, were listed in alphabetical order. Type species of genera and other species were first listed in their original generic designation. We provide keys to species for all three major groups of parastenocaridids treated in this monograph, as well as diagnoses for two genera (one of newly established here), but not a diagnosis for the *brevipes* group. The latter forms the core of the nominotypical genus *Parastenocaris*, as it contains its type species. Groups of species are not recognized as valid taxonomic categories by the International Code of Zoological Nomenclature. For all species we provide the following data: synynyms, type locality, deposition of types, specimens examined (if any), redescription, at least one plate of illustrations (in some cases also SEM photographs), distribution, ecology, and remarks (usually including notes on taxonomy and affinities). Some species redescriptions were made comparative, especially when dealing with very closely related congeners. In several species (where studied) sensilla on all somites (body segments) were numbered consequtively with Arabic numerals from anterior to posterior part of the body and from dosal to ventral side to aid recognision of homologous structures; they are not intended as a novel terminology. This monograph should provide at a glance an

overview of the development of standards of morphological examination of these tiny animals in the last century or so. We hope it will also serve as an inspiration for recollecting and redescribing many insufficiently described taxa, as well as for collecting in previously unexplored parts of the world.

Family Parastenocarididae Chappuis, 1940

Subfamily Fontinalicaridinae Schminke, 2010

Genus Proserpinicaris Jakobi, 1972 sensu Karanovic et al. (2012)

Nipponicaris Jakobi, 1972; Pannonicaris Jakobi, 1972.

Type species: Parastenocaris proserpina Chappuis, 1938.

OTHER SPECIES: Parastenocaris admete Cottarelli, Fasano, Mura and Saporito, 1980; Parastenocaris amalasuntae Bruno and Cottarelli, 1998; Parastenocaris cantabrica Chappuis, 1937; Parastenocaris cruzi Noodt and Galhano, 1969; Parastenocaris fontinalis meridionalis Rouch, 1990; Parastenocaris gorganensis Kovalchuk and Kovalchuk, 1990; Parastenocaris hispanica Martínez Arbizu, 1997; Parastenocaris ima Cottarelli, 1989; Proserpinicaris imjin Karanovic, Cho and Lee, 2012; Parastenocaris kalypso Pesce, Galassi and Cottarelli, 1988; Parastenocaris mangini Rouch, 1992; Parastenocaris moravica Šterba, 1965; Parastenocaris nicolasi Rouch, 1996; Parastenocaris nipponensis Chappuis, 1955; Parastenocaris ondali Lee and Chang, 2009; Parastenocaris pannonica Török, 1935; Parastenocaris phyllura Kiefer, 1938; Proserpinicaris wangpi Karanovic, Cho and Lee, 2012; Proserpinicaris pound Lee, 2012; Parastenovic, Cho and Lee, 2012.

DIAGNOSIS: Small to medium sized Fontinalicarididae, with cylindrical habitus, smooth cuticule, somites ornamted with few large sensilla, and with dorsal cuticular windows on cephalothorax and all urosomal somites, except first and last; spinules, if present at all, usually restricted to anal somite. Podoplean boundary between prosome and urosome inconspicuous. Genital complex in female occupying anterior ventral half of genital double somite; genital apertures and median copulatory pores covered by vestigial sixth legs, which fused completely into relatively narrow flap. Caudal rami cylindrical or leaf-like, with lateral cuticular pore near posterior margin, armed with seven elements (three lateral, one dorsal, and three apical); lateral elements inserted close to each other and much more anteriorly than dorsal seta; one lateral element minute and hard to observe between two others. Male antennula eight-segmented, prehensile, with geniculation between third and fourth and sixth and seventh segments; last two segments in line; distal anterior corner of seventh segment produced into very small spiniform process, but larger proximal spiniform process present on fifth segment on anterior surface; usually massive aesthetasc on fifth segment reaching tip of appendage. First swimming leg with no chitinous processes or inner basal armature. Second swimming leg with one-segmented endopod, armed with single slender seta apically, and with several apical spinules and sometimes with few lateral spinules. Third swimming leg endopod in female very small and linguiform segment, unarmed, usually with few apical spinules. Third swimming legs in male transformed into strong grasping organs, with large intercoxal sclerite between them, each composed of praexoca, coxa, basis, two-segmented exopod, and endopod reduced to single slender

armature element; basis and proximal exopodal segment robust, latter usually with beaks or chitinous lobes on inner margin; outer spine on first exopodal segment smooth, large, and curved; ancestral distal exopodal segment (apophysis) small, usually cylindrical, oriented slightly inwards, unornamented, and armed with single short element on top, which often leaf-like, or thumb-like. Fourth swimming leg in male with or without spinules on inner margin of coxa, but always with large and slender hyaline process on anterior surface of basis, between exopod and endopod, and no other chitinous structures on basis; first exopodal segment with longitudinal row of strong spinules on inner margin, and not other structures or depressions on this margin; endopod one-segmented, with or without apical armature, but usually curved and variously transformed, often knife-like (with serrated edges or tubarcules), rarely pinnate, sometimes with scoop-like structure on tip. Fourth swimming leg in female without hyaline process on basis or inner spinules on first exopodal segment; endopod also one-segmented but cylindrical, straight, and not transformed, with strong element on tip, several apical spinules, and several spinules around midlength close to inner margin. Fifth legs very similar in shape in male and female, elongated and simple triangular plates, with inner distal corner produced into spiniform precess, ornamented with spinules along inner margin (these often absent in female), usually another row of spinules on posterior surface proximally, and single large cuticular pore on anterior surface; armature consists of very long outermost seta (ancestral basal); two setae at outer base of inner distal process (probably ancestral endopodal seta), and sometimes small seta (or long spinule?) on posterior surface at base of basal seta; latter element most often reduced into minute spiniform process and hardly visible (smaller than most spinules). Sixth legs in male also fused (or right one reduced and left one enlarged?) smooth, unarmed, unornamented, forming simple operculum covering gonopore.

REMARKS: Fourth swimming leg in male with a large and slender hyaline process on the anterior surface of basis, between exopod and endopod, being sole chitinous structure on this segment, is a synapomorphy that unites all species included in the genus *Proserpinicaris* Jakobi, 1972 as redefined by Karanovic et al. (2012). Most other characters can be found in some other Fontinalicarididae genera, or species of *Parastenocaris* Kessler, 1913 that are currently considered to be members incertae sedis of this subfamily by Schminke (2010) (see the Introduction section above). Endopod of the fourth swimming leg in male is usually lanceolate or knife-like, with serrated margins, except in *Proserpinicaris ima* (Cottarelli, 1989), where it is completely smooth, and in *P. cruzi* (Noodt and Galhano, 1969) and *P. cantabrica* (Chappuis, 1937), where the endopod is pinnate (or plumose) along inner margin. Both conditions (plumose and smooth endopod) are probably secondary transformations and/or neotenic features, as a transformed endopod with serrulate or tuberculate margins can be found in some other unrelated taxa, and thus is probably a plesiomorphic character state in a larger group.

All five Asian species have the endopod of the fourth leg in male with a scoop-like structure, formed by a bunch of basally fused apical spinules, and form a monophyletic group of species. They all, however, have a very well developed hyaline process on the anterior surface of the forth leg basis, a complex structure and highly unlikely to have arisen convergently a number of times, which means that recognising the Asian group as a separate genus would render the genus *Proserpinicaris* paraphyletic. Type species of two genera proposed by Jakobi (1972) (*Nipponicaris* Jakobi, 1972, and *Pannonicaris* Jakobi, 1972) also share this structure, and were included by Karanovic et al. (2012) in the redefined genus *Proserpinicaris*, which makes these two genera junior subjective synonyms of *Proserpinicaris* (see above).

The genus *Proserpinicaris*, as redefined by Karanovic et al. (2012), is Palearctic in distribution, with its centre of diversity in southern Europe. We have to point out that the original description of *P. gorganensis* is severely lacking in detail (see Kovalchuk and Kovalchuk, 1990), but that is a constant

problem in this family (Schminke, 2010), and one of the main factors that precludes a meaningful cladistic analysis based on morphological characters (Karanovic, 2005a; Karanovic and Cooper, 2011a, b). Of the 20 species of Proserpinicaris, only probably those of P. amalasuntae, P. cruzi, P. hispanica, P. phyllura and P. proserina are adequate enough to allow recognizing potential new closely related congeners, and those of the latter two mostly thanks to some detailed redescriptions (see Kunz, 1938; Noodt, 1952; Bruno and Cottarelli, 1998). All other species would have to be redescribed at one stage or another, if we are to properly assess the diversity in this group and explore phenomena like short range endemism. Some other, also technical, problems are already mentioned in the Introduction section above. Karanovic et al. (2012) speculate that the male fourth leg of P. pannonica, as illustrated by Török (1935), was probably swapped with another new species that he described in the same paper and from the same locality (Budapest, Hungary), Parastenocaris budapestensis Török, 1935. This mix-up caused quite a few problems in the past. Lang (1948), for example, because of this, and because he relayed mostly on characters of the fourth swimming leg, placed *P. budapestensis* in the proserpina group, although it shared hardly any other morphological characters with other four species. Similarly, he considered *P. pannonica* to be a member of the *minuta* group. The same original mix-up prompted Jakobi (1972) to designate P. pannonica the type species of his new genus Pannonicaris Jakobi, 1972, where he additionally included four other species from the minuta group. He also designated *P. budapestensis* the type species of his new genus *Lacustricaris* Jakobi, 1972, where he additionally included only a completely unrelated Canadian species, Parastenocaris lacustris Chappuis, 1958. Schminke (2010) recognized that P. budapestensis and P. lacustris are so different that he included them in two separate subfamilies, but unfortunately did not realize that by excluding the type species from the genus Lacustricaris it cannot be a valid genus any longer. Karanovic et al. (2012) formally synonymized Lacustricaris with Parastenocaris Kessler, 1913, and designated P. lacustris as incertae sedis in Fontinalicaridinae.

Karanovic et al. (2012) also did not consider *Parastenocaris nolli* Kiefer, 1938, and *P. delamarei* Chappuis, 1958 as members of the genus *Proserpinicaris*, even though they were included in that genus by Jakobi (1972). The former species has its lateral caudal setae inserted near posterior margin, very short fifth legs both in male and female, and relatively small spinules on the male fourth leg basis inserted medially from endopod, among many morphological differences (see Kiefer 1938, 1960a, b), and it was placed in the nominotypical subfamily by Schminke (2010). *Parastenocaris delamarei* was also placed in the nomynotypical subfamily by Schminke (2010), and it differs from all 20 species of *Proserpinicaris* by the shape of the male third leg, armature of the male fourth leg basis, and insertion of lateral setae on the caudal rami (see Chappuis and Delamare Deboutteville, 1958). Here we designate a new genus for these and few other probably closely related species (see below).

Martínez Arbizu (1997) noted that his newly described Spanish species, *P. hispanica*, is morphologically extremely similar to the French *Parastenocaris fontinalis meridionalis* Rouch, 1990, and he argued that the latter is a separate species too, rather than a subspecies of *P. fontinalis* Chappuis and Schnitter, 1915. We completely agree with this view. We do not, however, share his view that *P. hispanica* and *P. meridionalis* should be considered members of the *fontinalis* group, which was already pointed out by Karanovic (2005a) and Karanovic et al. (2012). Martínez Arbizu's (1997) phylogenetic analysis was conducted on an arbitrary group of four species and one subspecies (including *Parastenocaris psammica* Songeur, 1961, which has a completely different fifth legs both in male and female), and without an outgroup. Although he mentioned that *Parastenocaris aquaductus* Chappuis, 1925 was "considered an appropriate outgroup to polarize the characters", no characters were scored for it in his matrix, nor did it appear on the resulting cladogram. Furthermore, of the 16 scored characters six have the same state in all five taxa, and thus are not phylogenetically infor-

mative for that analysis. Most curiously, he did not score for the presence/absence of a large hyaline process on the male fourth leg basis, an obvious morphological feature that at once distinguishes P. hispanica and P. meridionalis from the other three members, and which was used by Lang (1948) to define a completely separate group of species (the proserpina group). Had he done so, he would have to consider a much larger number of species in his phylogenetical analysis. It is not clear why Martínez Arbizu (1997) choose to compare his new species with a selected small number of species from the fontinalis group (which has grown significantly since first proposed by Lang (1948)), and none from the *proserpina* group, but we speculate that may be because of a relatively similar shape of the male fourth leg endopod in *P. proserpina* and *P. hispanica*. Unfortunately, as we discussed above, the transformed endopod with serrulate or tuberculate margins can be found in some other unrelated taxa (see, for example, Cottarelli et al., 2000), and is a plesiomorphic character state. Proserpinicaris meridionalis and especially P. hispanica show a number of plesiomorphic features in the genus, including the inner spinules on the male fourth leg coxa, long spinule (or small seta?) on the posterior surface of the fifth leg at base of basal seta, long and basally placed tubular pore on the inner margin of the first exopodal segment in male third leg, and relatively small hyaline process on the male fourth leg basis (considerably shorter than endopod). We should mention here that there is a possibility that Martínez Arbizu (1997) overlooked at least one species in the P. hispanica complex, which we induce from his drawings of the female leaf-like caudal rami and male anal somite with ventral spinules in a specimen from Sta. Rouch 1978 n° 8 (see his Figs. 6B, 7B).

Schminke (2010) added further to the problem, by providing a series of drawings of the typical Parastenocaridinae and Fontinalicaridinae, without any reference for their specific identity, origin of the material, or its deposition. Although, he did not say it specificly, reading through his paper one may be lead to think that his Fig. 2D is of *P. fontinalis*, although it shows a large hyaline process on the anterior surface of the male fourth leg basis, i.e. looks very much like that of *P. hispanica*. This could be quite accidental, but we should mention here that in the original description of *P. fontinalis* by Schnitter and Chappuis (1915), all subsequent redescriptions (Noodt, 1952; Kiefer, 1959; Kulhavyý, 1961; Songeur, 1961; Dussart, 1966), and even in the description of a separate subspecies (Kiefer, 1960c), the male fourth leg basis is completely smooth. Although it is beyond the scope of this monograph to formally redefine the genus Fontinalicaris Jakobi, 1972, we can suggest that at least the following six taxa form a morphologically compact and probably monophyletic group with F. fontinalis (Schnitter and Chappuis, 1915), its type species: F. bohemica (Šterba, 1968) n. comb. from the Czech Republic (Šterba, 1968); F. chappuisi (Serban, 1960) n. comb. from Romania (Serban, 1960); F. fontinalis borea (Kiefer, 1960) from Germany (Kiefer, 1960c); F. kabyloides (Enckell, 1965) n. comb. from Spain (Enckell, 1965); F. ruffoi (Chappuis, 1954) n. comb. from Italy (Chappuis, 1954); and F. torokae (Ponyi, 1957) from Hungary (Ponyi, 1957). Fontinalicaris bohemica was synonymized with F. fontinalis by Martínez Arbizu (1997), but this is questionable in the light of discovering short range endemism in this group more as a rule that as an exception (Karanovic and Cooper, 2011a, b; Karanovic et al., 2012). We are in a complete agreement with Martínez Arbizu's (1997) view that Parastenocaris phyllophora Noodt, 1954 is not at all closely related to Fontinalicaris fontinalis, although it was included in the genus Fontinalicaris by Jakobi (1972) as its only other member beside the type species. Actually, P. phyllophora was considered a synonym of P. italica Chappuis, 1935 already by Chappuis (1958, 1959) and Kiefer (1963, 1968), but the latter was designated by Jakobi (1972) as the type species of another genus, Italicocaris Jakobi, 1972. This is probably one of the best illustrations of the superficial nature of the family revision done by Jakobi (1972), and the problems we have to deal with while reinstating and redefining his genera. There is no question that the genera Proserpinicaris and Fontinalicaris are relatively closely related, but so are some other Fontinalicaridinae. For example, the South American

genus *Brasilibathynellocaris* Jakobi, 1972 has the same pattern of urosomal cuticular windows, insertion of the lateral caudal setae, inner coxal spinules on the male fourth leg, fifth legs with minimal sexual dimorphism, and even relatively similar structure of the male third leg, but differs from *Proserpinicaris* and *Fontinalicaris* by the transformation of the first exopodal segment of the male fourth leg (see Noodt, 1962).

1. Proserpinicaris admete Cottarelli, Fasano, Mura and Saporito, 1980 (Fig. 1)

Parastenocaris admete Cottarelli et al., 1980, p. 619, figs. 1-17.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 400 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. No information available on somite ornamentation. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, reaching distal margin of first antennular segment, about as long as wide.

Anal somite (Fig. 1A) ornamented only with posterior row of small spinules laterally, and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with almost straight and smooth distal margin, reaching posterior end of anal somite, representing 60% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, one of which on internal margin of anal operculum basally.

Caudal rami (Fig. 1A, B) about 2.3 times as long as greatest width (dorsal view) and about 0.7 times long as anal somite, mostly cylindrical but with inflated central part, slightly divergent, with space between them about one ramus width, unornamented; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about 0.7 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 2/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.7 times as long as ramus, and only slightly longer than distal seta. Inner apical seta small, smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about five times as long as ramus. Outer apical seta also without breaking plane and relatively strong basally but much shorter, slightly shorter than caudal ramus.

Antennula (Fig. 1D) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to much longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (certainly incomplete): 0.3.6.1.0.0.5. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 1E) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis partly divided, about 3.5 times as long as wide, unarmed, ornamented with two short rows of large spinules on anterior surface.

Endopod about 0.6 times as long as allobasis and 2.2 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, which twice as long as segment.

Mandibula (Fig. 1F) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula unknown.

Maxilla (Fig. 1G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with one endite, armed with two setae apically. Basis drawn out into strong and pinnate claw, without seta at base. Endopod represented by minute segment, which basally fused to basis, armed with single smooth apical seta.

Maxilliped (Fig. 1H) with very short but strong syncoxa, unarmed and unornamented; basis slender, about four times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 1I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and only slightly longer than larger geniculate exopodal seta.

Second swimming leg (Fig. 1J, K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with slender outer seta, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.1 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical, about five times as long as wide, reaching midlength of first exopodal segment, ornamented with two large spinules on outer margin and several large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 1L) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with row of minute spinules along inner margin proximally and with many larger spinules or tubercules on anterior surface distally. Endopod small, spiniform and smooth. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards, and with two large chitinous bulbs on inner margin proximally, ornamented with very large spinule at base of chitinous bulb, close to inner margin; armed subapically with spatulate, strong, and smooth spine, which significantly longer than apophysis and curved inwards; ancestral distal segment (apophysis) cylindrical, also oriented inwards, unornamented



Fig. 1. *Proserpinicaris admete*. Male: A. anal somite and caudal rami, dorsal view; B. left caudal ramus, lateral view; C. right caudal ramus of another specimen, lateral view; D. antennula; E. antenna; F. mandibula; G. maxilla; H. maxilliped; I. first swimming leg; J. basis and endopod of second swimming leg; K. basis and exopod of second swimming leg; L. third swimming leg; M. exopod of fourth swimming leg; N. basis and endopod of fourth swimming leg; O. fifth leg. Female: P. left caudal ramus, lateral view; Q. distal part of antennula; R. second swimming leg without last two exopodal segments; S. third swimming leg without last two exopodal segments; T. exopod of third swimming leg; U. fourth swimming leg without last exopodal segment and any exopodal armature/ornamentation; V. fifth legs. Scales: 25 μ m (cited from Cottarelli et al., 1980, modified).

and armed with single short smooth seta on top.

Fourth swimming leg (Fig. 1M, N) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge curved chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.8 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes proximally and distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 1O) simple triangular cuticular plate, inner distal corner produced into long smooth spiniform process, 3.8 times as long as greatest width, ornamented with several spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; middle seta (ancestral outer endopodal) 0.2 times as long as leg, and about as long as innermost seta (ancestral inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 408 to 430 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite. Other information on somites shape and ornamentation missing.

Caudal rami (Fig. 1P) very similar to male, but less inflated in lateral view.

Antennula (Fig. 1Q) also seven-segmented but not geniculate, unornamented, with slender aesthetasc on fourth segment, not reaching tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (probably incomplete): 0.3.4.2.0.0.5. All setae, except proximalmost one on second segment, smooth..

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 1R), and exopod of fourth swimming leg (Fig. 1U) similar to male.

Third swimming leg (Fig. 1S, T) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, small, linguiform, unornamented and unarmed.

Fourth swimming leg (Fig. 1U) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, not distinct at base, smooth, and about 0.8 times as long as endopod; endopod with apical spine reaching beyond posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 1V) also simple cuticular plate, but with inner distal corner more produced posteriorly and without armature on inner margin. Armature same as in male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: The type material is deposited in the first author's working collection in the Dipartimento

di Scienze Ambientali, Università della Tuscia, Viterbo.

TYPE LOCALITY: Italy, Sardinia, Sassari Province, Bassacutena village, Liscia River, interstitial on the banks.

DISTRIBUTION: This species is known from nine different creeks and rivers in Sardinia, Italy.

ECOLOGY: All specimens were obtained from interstitial habitats of the banks of rivers and creeks, mostly using the Karaman-Chappuis method, but also with a hyporheic pump. The species seems to be widely distributed in most interstitial habitats in Sardinia, although absent from Isola la Maddalena island (northern part of Sardinia), where it is replaced by the closely related *P. ima*.

REMARKS: Cottarelli et al. (1980) considered *P. admete* to be morphologically most similar to *P. prosepina*, but observed enough morphological differences in the shape and ornamentation of the third leg in male to be able to justify a new species. The former is endemic to Sardinia, while the latter is relatively widely distributed in central parts of the mainland Italy. *Proserpinicaris ima*, described from the tiny Isola la Maddalena island (northern part of Sardinia), is also closely related to these two species, and they have all probably originated from the same ancestor with a wider distributional range (Cotarelli, 1989). This species is a short-range endemic, and its main morphological characters are outlined below.

2. Proserpinicaris amalasuntae Bruno and Cottarelli, 1998 (Fig. 2)

Parastenocaris admete Cottarelli et al., 1980, p. 619, figs. 1-17.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 404 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about 8.8; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow, and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites (Fig. 2A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax about 1.6 times as long as wide in dorsal view; representing 20% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally not known.

Urosomal somites (except preanal, unornamented) with eight posterior sensilla and with smooth hyaline fringes.

Anal somite (Fig. 2A, B) ornamented only with posterior row of small spinules laterally, and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with strongly concave and smooth distal margin, not reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, one of on internal margin of anal operculum basally.

Caudal rami (Fig. 2A, B) about 2.3 times as long as greatest width (dorsal view) and almost 0.7 times as long as anal somite, mostly cylindrical but slightly narrowing towards distal end and bulging in proximal part on inner side, divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/4 of ramus length. Proximalmost lateral seta placed more dorsally, 0.7 times as long as ramus, about three times as long as middle seta (minute), and 1.5 times as long as distalmost (ventralmost) one. Inner apical seta strongest, without breaking plane, smooth, about twice as long as outer apical seta and three times as long as ramus. Outer apical seta also without breaking plane but unipinnate, relatively strong basally. Caudal rami shape variable, and sometimes even asymmetrical.

Antennula (Fig. 2C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.6.5.3.0.0.7. All setae slender and all except largest seta on second segment smooth.

Antenna as in *P. proserpina*.

Mandibula (Fig. 2D) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 2E) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide in lateral view, unornamented but armed with strong lateral seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two smooth apical setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 2F) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong pinnate claw, probably without seta at base (although drawn in original line drawings; not seen in SEM photos). Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 2G) with very short but strong syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 2H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on inner margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all

segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.3 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 2I) with smooth praecoxa, and intercoxal sclerite. Coxa with posterior row of minute spinules. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.2 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about eight times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along apical margin and two on outer margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 2J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin; additional few small spinules on anterior surface. Endopod minute but distinct segment, curved, about as long as largest spinule on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with two large chitinous beaks on inner margin distally, unornamented, armed subapically with simple, strong, smooth and curved spine, significantly longer than apophysis; ancestral distal segment (apophysis) conical, oriented slightly outwards, unornamented and armed with single minute seta on top.

Fourth swimming leg (Fig. 2K, L, M) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 1.2 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes proximally and distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 2N) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, ornamented with several spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.4 times as long as entire leg; middle seta (ancestral outer endopodal) shortest, 0.3 times as long as leg, and 0.7 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 405 μ m in paratype. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite slightly longer than wide (dorsal view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from



Fig. 2. *Proserpinicaris amalasuntae*. Male: A. last two urosomal somites and caudal rami, dorsal view; B. anal somite and right caudal ramus, lateral view; C. antennula; D. mandibula; E. maxillula; F. maxilla; G. maxilliped; H. first swimming leg; I. second swimming leg; J. third swimming legs; K. fourth swimming leg, with last two exopodal segments not drawn on one leg; L, M. fourth swimming leg, without last two exopodal segments, different specimens; N. fifth leg. Female: O. distal part of antennula; P. third swimming leg; Q. fourth swimming leg, without last two exopodal segments; R. fifth legs. Scales: 25μ m (cited from Bruno and Cottarelli, 1998, modified).

fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami very similar to male, and only slightly longer in proportion to anal somite and with somewhat more slender anterior part.

Antennula (Fig. 2O) also seven-segmented, unornamented, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula: 0.4.4.2.1.0.7. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 2Q) similar to male.

Third swimming leg (Fig. 2P) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with single spinule apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 2Q) without spiniform process on basis. Endopod one-segmented, ornamented with several spinules on outer margin and transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, and about 0.9 times as long as endopod; endopod with apical spine reaching slightly beyond posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 2R) also simple cuticular plate, but with inner distal corner more produced posteriorly and without spinules along inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material deposited in the Dipartimento di Scienze Ambientali, Università della Tuscia, Viterbo.

TYPE LOCALITY: Italy, Latio, Bolsena Lake, beach about 2 km north-west from Capodimonte.

DISTRIBUTION: This species is known only from the type locality, Bolsena Lake, as well as from the following three additional localitites: Fiora River near Sovana (Grosseto), Fiora River near Vulci (Viterbo), and a well on the Maciano-Farnese road (Grosseto); all in Italy.

ECOLOGY: Specimens were obtained from wells, hyporheic, and groundwater habitats, as well as from lake beaches, mostly using the Karaman-Chappuis method. This tells us about its wide ecological tolerance for many environmental factors, such as dissolved oxygen, temperature, water movement, and even water chemistry. Interestingly, its type locality is a volcanic lake, some 300,000 years old, but the species could have colonised this virgin habitat easily from the surrounding terrain.

REMARKS: Bruno and Cottarelli (1998) noted that *P. amalasuntae* is probably most similar morphologically to *P. proserpina*, with which it can even be found sympatrically in some localities in Italy. The main differences include the fine details in shape and ornamentation of the male third and fourth legs, which are sexually dimorphic characters. The endopod of the fourth legs seems to be

the main distinguishing feature between these two related taxa, as it is much longer and more robust in *P. amalasuntae* (i.e., as long as or slightly longer than the first exopodal segment).

3. Proserpinicaris cantabrica Chappuis, 1937 (Fig. 3)

Parastenocaris cantabrica Chappuis, 1937, p. 569, figs. 39-45; Lang, 1948, p. 1243, fig. 499-3; Dussart, 1967, p. 418, fig. 184.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 400 μ m. Preserved specimen colourless. Nauplius eye absent. Body about nine times as long as wide, composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. No information available on somite ornamentation, or rostrum. Anal operculum convex and long, but not reaching posterior margin of anal somite.

Caudal rami about as long as anal segment, four times as long as greatest width (dorsal view), cylindrical, unornamented, armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about as long as caudal ramus width, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/4 of ramus length, of about same length, also about as long as ramus width. Inner apical seta small, smooth, inserted more ventrally, about as long as lateral setae. Middle apical seta strongest, without breaking plane, smooth, 2.3 times as long as caudal ramus. Outer apical seta very small, hardly longer than dorsal seta and only slightly longer than ramus width.

Antennula, antenna, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown but probably similar to type species.

Second swimming leg (Fig. 3A) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed and unornamented. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one longest; all exopodal armature bipinnate. Endopod one-segmented, cylindrical, about five times as long as wide, reaching midlength of first exopodal segment, ornamented with one large spinule on outer margin and at least two large spinules on apical margin; armed apically with one smooth seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 3B) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta, ornamented with diagonal row of large spinules along outer margin proximally. Endopod small, spiniform and smooth. Exopod with both segments fused; ancestral proximal segment three times as long as wide, curved inwards, and with one small chitinous beak on inner margin proximally, unornamented, armed subapically with spiniform, slender, and smooth spine, slightly longer than apophysis and pointing distally; ancestral distal segment (apophysis) cylindrical, also oriented inwards, unornamented and unarmed, finished with broad hyaline structure.

Fourth swimming leg (Fig. 3C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all



Fig. 3. *Proserpinicaris cantabrica*. Male: A. second swimming leg without last two exopodal segments; B. third swimming leg; C. fourth swimming leg without two last exopodal segments; D. fifth leg. Female: E. anal somite and left caudal ramus, dorsal view; F. fifth leg; G. fourth swimming leg without last two exopodal segments. Scales: unknown (cited from Chappuis, 1937, modified).

segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta. Endopod one-segmented and spiniform, but with serrulate inner margin, resembling cutting blade.

Fifth leg (Fig. 3D) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, three times as long as greatest width, ornamented with several large spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost half as long as entire leg; middle seta (ancestral outer endopodal) smallest, 0.25 times as long as outermost seta, and about 0.8 times as long as innermost seta (ancestral inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 400 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite. Other information on somites shape and ornamentation missing.

Caudal rami, antennula, antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 3G) similar to male.

Third swimming leg with large praecoxa, smooth coxa and intercoxal sclerite. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, small.

Fourth swimming leg (Fig. 3G) without spiniform process on basis. Endopod one-segmented, spiniform, unornamented but armed apically with single bipinnate spine, fused to segment basally, not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 3F) similar to that in male, but without spinules on inner margin, and additionally ornamented with large spinule (or small seta) at base of outermost seta.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: Spain, Santander, Cueva de Santin cave, dripwater pools.

DISTRIBUTION: This species is known from the type locality only, Cueva de Santin cave near Santander, Spain.

ECOLOGY: All specimens were collected from dripwater pools in a cave, which probably means that this is a stygobiont species adapted to live in deeper subterranean environments. No other information on the environmental factors at the time of collecting were given, but this being a cave in northern Spain probably means temperatures between 11 and 13°C in early October, when the specimens were collected.

REMARKS: Lang (1948) classified this species in the *proserpina*-group, based on the shape of the fourth leg basis and endopod in male. Clearly it is closely related to a number of European species from this complex, especially to those from Italy, but it can be distinguished from all by the shape of the third leg in male and to a certain extent the shape and armature of the caudal rami. Unfortunately, the original description is lacking in detail, so many morphological characters cannot be compared with other congeners.

4. *Proserpinicaris cruzi* Noodt and Galhano, 1969 (Fig. 4)

Parastenocaris cruzi Noodt and Galhano, 1969, p. 69, fig. 24.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), about 530 μ m. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome; body length/width ratio from eight to nine. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores, spinules present only on anal somite, caudal rami and appendages, dorsaly round cuticular window present at least on preanal somite (Fig. 4A). Rostrum, cephalothorax, and detailed ornamentation and shape of free prosomite and first three urosomites unknown. Preanal somite illustrated with dorsal sensillum (Fig. 4C), but only in lateral view and could be a mistake or bacterial growth.

Anal somite (Fig. 4A–C) ornamented only with pair of large dorsal sensilla at base of anal operculum and with four posterior ventral spinules at base of each caudal ramus. Anal operculum well developed, unornamented on outer surface, with strongly convex and smooth distal margin, not reaching posterior end of anal somite, representing 65% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 4A–C) about four times as long as greatest width (dorsal view) and almost 1.2 times as long as anal somite, mostly cylindrical but slightly tapering posteriorly, strongly divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical; note: smallest lateral element not illustrated but probably too small to be observed easily). Ornamentation consists of several ventral spinules along posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6 of ramus length, about as long as caudal ramus, probably triarticulate basally (although only one pseudojoint illustrated). Lateral setae thin and smooth, inserted close to each other but at 2/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.7 times as long as ramus, and about 1.7 times as long as ramus. Middle apical seta strongest, without breaking plane, unipinnate, about half as long as entire body, pointing posteriorly. Outer apical seta also without breaking plane and unipinnate, but much shorter, only about 1.2 times as long as caudal ramus, pointing latero-posteiorly.

Antennula (Fig. 4C) relatively long, seven-segmented, prehensile and digeniculate, ornamented only with few spinules on first segment. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender and short aesthetasc on fourth segment not base of last segment, fused basally to much longer seta. Much shorter and even more slender apical aesthetasc on seventh segment, fused basally to two setae. Setal formula: 0.5.4.5.0.1.9. All setae slender and all, except largest seta on second segment and one seta on fourth segment, smooth.

Antenna composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis reported to be armed with one seta and ornamented with one spinule, but they probably both ornamentation rather than armature. Exopod minute, cylindrical, unornamented but armed with single apical unipinnate seta.

Mandibular palp one-segmented, cylindrical, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula without exopod or endopod, but no other details described.

Maxilla reported with three endites, but most probably as in other congeners, composed of syncoxa, basis, and one-segmented endopod, and yyncoxa with two endites,

Maxilliped slender, with short but strong syncoxa, long and slender, and endopod represented by long curved claw, swollen at base as indication of ancestral one-segmented endopod.

First swimming leg (Fig. 4E) with smooth praecoxa, coxa and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on posterior margin at base of endopod, and several spinules on inner margin; armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner



Fig. 4. *Proserpinicaris cruzi*, Male. A. last two urosomal somites and caudal rami, dorsal view; B. anal somite and right caudal ramus, ventral view; C. last two urosomal somites and left caudal ramus, lateral view; D. antennula; E. first swimming leg; F. second swimming leg; G. third swimming leg; H. fourth swimming leg. Scales: 100 μ m (cited from Noodt and Galhano, 1969, modified).
distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.1 times as long as longer geniculate exopodal seta.

Second swimming leg (Fig. 4F) with smooth praecoxa, coxa and intercoxal sclerite.. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about 5.7 times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with several large spinules along apical margin and one on outer margin; armed apically with one smooth seta, which about as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 4G) with smooth praecoxa, coxa, and intercoxal sclerite. Basis veru robust, about twice as long as coxa, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod represented by slender and long seta, inserted at about 2/3 of basis length. Exopod with both segments fused; ancestral proximal segment twice as long as wide, slightly curved inwards and, with blunt proximal chitinous beak on inner margin, ornamented with two large spinules on outer margin distally, armed subapically with simple, strong, smooth and slightly outwardly curved spine, which significantly longer than apophysis; ancestral distal segment (apophysis) thumb-like, oriented inwards, unornamented and unarmed, with thin cuticulum apically and blunt tip.

Fourth swimming leg (Fig. 4H) with smooth praecoxa, coxa and intercoxal sclerite. Basis armed with single outer seta, ornamented only with large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and about 2.6 times as long as outer spine. Endopod one-segmented, small and unornamented, armed apically with single long and strong element; apical element plumose along inner margin and partly along outer margin distally; endopod with apical element nearly reaching distal margin of first exopodal segment.

Fifth leg (Fig. 4I) simple triangular cuticular plate, 2.5 times as long as wide, inner distal corner produced into very short and smooth spiniform process, ornamented with long row of spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, 0.6 times as long as entire leg; second seta (ancestral outer endopodal) 0.3 times as long as leg, and 1.6 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth leg triangular. **Female**: Unknown.

TYPE: Type material probably lost.

TYPE LOCALITY: Portugal, Braga District, Barcelos Municipality, Rio Cávado, interstitial water.

DISTRIBUTION: This species is known from the type locality only, a small river (Rio Cávado) in northern Portugal.

ECOLOGY: The species was collected from interstitial waters, along with two other parastenocaridids, three different species of bathynellids, and unidentified canthocampthid harpacticoids, cyclopoids, and ostracods (Noodt and Galhano, 1969). This is a typical interstial subterranean suite of crustaceans, and there is very little doubt that *P. cruzi* is a proper stygobiont and probably also a short range endemic. Although it was only collected at the type locality, two other parastenocaridids were found additionally at Rio Mondego, some 100 km to the south. It is possible that *P. cruzi* has somewhat wider range too, as many parastenocaridids identified only to the genus level (probably juveniles) were reported by Noodt and Galhano (1969) from Rio Lima (ca. 30 km to the north of the type locality), Rio Douro (ca. 50 km to the south of the Type locality), as well as from Rio Mondego.

REMARKS: Noodt and Galhano (1969) assigned their new species to the *proserpina* group and provisionally discussed its differences with supposedly closely related *P. cantabrica*. However, *P. cruzi* differs from *P. cantabrica*, as well as from all other species of *Proserpinicaris*, by its richly plumose apical endopodal armature element on the fourth leg in male, and additionally by the presence of three large dorsal spinules on caudal rami. Both are plesiomorphic features and can be found in some South American genera. It seems that this species has no close relatives among known congeners. Females of this species are still unknown, which makes it very difficult to judge its phylogenetic relationships.

5. Proserpinicaris gorganensis Kovalchuk and Kovalchuk, 1990 (Fig. 5)

Parastenocaris gorganensis Kovalchuk and Kovalchuk, 1990, p. 75, figs. 1, 2.

Male: Total body length unknown. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 5A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about nine; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, probably ornamented with sensilla and pores (no spinules), presence of cuticular windows unknown.

Cephalothorax (Fig. 5A) about 1.5 times as long as wide in dorsal view; representing 16 % of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally unknown, as well as those of other somites.

Anal somite (Fig. 5B) probably ornamented with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with concave and smooth distal margin, almost reaching posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 5A, B) almost three times as long as greatest width (dorsal view) and about as long as anal somite, cylindrical, divergent, with space between them about 1.5 times one ramus width, unornamented; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about as long as caudal



Fig. 5. *Proserpinicaris gorganensis*, Male. A. habitus, dorsal view; B. last two urosomal somites and right caudal ramus, lateral view; C. antennula; D. antenna; E. first swimming leg; F. second swimming leg; G. third swimming leg; H. fourth swimming leg; I. fifth leg. Scales: unknown (cited from Kovalchuk and Kovalchuk, 1990, modified).

ramus, triarticulate basally. Lateral setae slender and smooth, inserted close to each other but at 2/5 of ramus length. Proximal lateral seta placed more dorsally, 0.7 times as long as ramus, and about 1.3 times as long as distal one. Inner apical seta smooth, inserted more ventrally, about as long as ramus. Middle apical seta strongest, without breaking plane, smooth, exact length unknown, but significantly longer than ramus. Outer apical seta also without breaking plane and smooth, relatively strong basally but much shorter, about 1.5 times as long as ramus.

Antennula (Fig. 5C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Long and slender aesthetasc on fourth segment reaching tip of appendage, fused basally to slightly longer seta. Much shorter and more slender apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.3.1.2.0.0.8. All setae slender and smooth.

Antenna (Fig. 5D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod,

and one-segmented exopod. Coxa very short, unornamented. Allobasis about four times as long as wide, unarmed but ornamented with one large spinule proximally on anterior surface. Endopod half as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula, maxillula, maxilla, and maxilliped unknown, but possibly similar to type species. First swimming leg (Fig. 5E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 5F) with smooth praecoxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin and few spinules at base of endopod. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.5 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, about five times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with few large spinules along apical margin; armed apically with one smooth seta, about as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 5G, J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, ornamented with row of large spinules along outer margin, armed with outer long and slender seta. Endopod possibly absent, or not observed. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and with large chitinous beak on inner margin proximally, ornamented with several large spinules on outer margin proximally, armed subapically with simple, strong, smooth and sharp spine, about as long as apophysis; ancestral distal segment (apophysis) conical, oriented slightly inwards, unornamented and armed with single short apical spine, smooth.

Fourth swimming leg (Fig. 5H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with huge chitinous inwards-pointing spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, additionally ornamented with long and slender spinule on inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 1.4 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, curved outwards, with serrated outer margin distally.

Fifth leg (Fig. 5I) simple triangular cuticular plate, inner distal corner produced into long and smooth spiniform process, ornamented with several long spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, 0.3 times as long as leg and 1.25

times as long as two other setae (ancestral endopodal), which are subequal.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: unknown.

TYPE: Type material deposited in the Hydrobiological Institute, Kiev, Ukraine.

TYPE LOCALITY: Ukraine, Zakarpatska district, Tyacev region, Lopukhovo village, spring.

DISTRIBUTION: This species is only known from the type locality, Lopukhovo village in Ukraine, from an altitude of about 1,400 m above sea level.

ECOLOGY: The specimens were obtained in a cave, but precise environment and environmental conditions are unknown.

REMARKS: Kovalchuk and Kovalchuk (1990) compared their new species only to *P. conimbrigensis* Noodt and Galhano, 1969, stating only that they are closely related and giving some major morphological differences. They also noted some similarities with *P. cornuta* Chappuis, 1955. Unfortunately, their drawings and descriptions are so basic that we can hardly say anything about this species, other than that it probably belongs to the family Parastenocarididae Chappuis, 1940, and that the shape of the fourth leg in the male, as drawn on one side, may suggest its place in the genus *Proserpinicaris*. This would be further supported by the shape and armature of the caudal rami. Any other conclusions will have to await re-examination of the type material. Karanovic et al. (2012) included this species provisionally in the genus *Proserpinicaris*.

6. Proserpinicaris hispanica Martínez Arbizu, 1997 (Fig. 6)

Parastenocaris hispanica Martínez Arbizu, 1997, p. 216, figs. 2-7.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 380 μ m in holotype. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 6A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.9; greatest width at posterior end of cephalothorax. Body length/width ratio about 8.8; cephalothorax about 1.1 times as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites (Fig. 6A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum (Fig. 6C) small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax about 1.7 times as long as wide in dorsal view; representing 19% of total body length. Ornamentation of surface of cephalic shield with sensilla quite sparse, dorsally with six large sensilla

around cuticular window. Second, fourth, and fifth pedigerous somites and genital somite with dorsal cuticular pore in anterior part. Each free somite with smooth hyaline fringe and ornamented with six or eight sensilla, except preanal somite, which lacks ornamentation (except dorsal cuticular window), and anal somite.

Anal somite (Fig. 6A, B) ornamented only with small cuticular pore antero-laterally, and with pair of large dorsal sensilla at base of anal operculum; one specimen with two strong spinules ventrally at base of caudal rami. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 6B) about 3.4 times as long as greatest width (lateral view) and almost 0.9 times as long as anal somite, mostly cylindrical but slightly inflated posteriorly, slightly divergent, with space between them about 1.2 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/3 of ramus length. Proximalmost lateral seta placed more dorsally, 0.8 times as long as ramus, about 10 times as long as middle seta (minute), and 3.5 times as long as distalmost (ventralmost) one. Inner apical seta small, smooth, inserted more ventrally, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 4.5 times as long as outer apical seta and 3.6 times as long as ramus. Outer apical seta also without breaking plane but unipinnate, relatively strong basally.

Antennula (Fig. 6C) relatively long, seven-segmented, prehensile and digeniculate, ornamented only with few spinules on first segment. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.4.3.5.0.0.9. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 6D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed and unornamented. Endopod about 0.6 times as long as allobasis and 2.2 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical unipinnate seta, twice as long as segment.

Mandibula (Fig. 6E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 6F) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 6G) ornamented with few spinules on inner margin basally, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single

smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong and pinnate claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 6H) with very short but strong syncoxa, unarmed and unornamented; basis slender, about four times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 6I) with smooth praecoxa and intercoxal sclerite. Coxa ornamented with transverse row of minute spinules on anterior surface, unarmed. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on posterior margin at base of endopod, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.3 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 6J) with smooth praecoxa, and intercoxal sclerite. Coxa with row of minute spinules on outer margin, unarmed. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about 3.7 times as long as wide, reaching midlength of first exopodal segment in length, ornamented with three large spinules along apical margin and two on outer margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 6K, L) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod minute, spiniform, about as long as spinules on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with two large chitinous beaks on inner margin proximally, ornamented with two large spinule on outer margin proximally and tube pore on inner margin, armed subapically with simple, strong, smooth and outwardly curved spine, which significantly longer than apophysis; ancestral distal segment (apophysis) thumb-like, oriented inwards, unornamented and armed with single short smooth spine on top.

Fourth swimming leg (Fig. 6M) with smooth praecoxa and intercoxal sclerite. Coxa unarmed, ornamented with bunch of spinules on inner margin. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.9 times as long as entire exopod and about twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately



Fig. 6. *Proserpinicaris hispanica*. Male: A. habitus, dorsal view; B. anal somite and left caudal ramus, lateral view; C. antennula and rostrum; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. exopod of third swimming leg, different specimen; M. fourth swimming leg; N. fifth leg. Female: O. fifth pedigerous somite with fifth legs and genital double somite, ventral view; P. left caudal ramus, lateral view; Q. antennula; R. endopod of second swimming leg; S. third swimming leg; T. fourth swimming leg. Scales: $A=100 \mu m$, $B-T=10 \mu m$ (cited from Martínez Arbizu, 1997, modified).

decorated with serrulate membranes proximally and distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 6N) simple triangular cuticular plate, three times as long as wide, inner distal corner produced into short and smooth spiniform process, ornamented with several spinules along inner margin at midlength, armed with four smooth setae; outermost seta (ancestral basal one) longest, 0.85 times as long as entire leg; next seta (ancestral exopodal) much smaller, 0.2 times as long as outermost seta and inserted close to it; third seta (ancestral outer endopodal) 0.3 times as long as leg, and 1.5 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 380 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite (Fig. 6O) about as long as wide (ventral view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles relatively large but difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami very similar to male, but in some females variable and inflated in anterior part from lateral view (Fig. 6P).

Antennula (Fig. 6Q) also seven-segmented but not geniculate, with slender aesthetasc on fourth segment, reaching tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (possibly incorrect): 0.4.5.2.1.1.9. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 6R), and exopod of fourth swimming leg (Fig. 6T) similar to male.

Third swimming leg (Fig. 6S) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with few spinules apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 6T) without spiniform process on basis. Endopod one-segmented, ornamented with several spinules on inner (?) margin and transverse apical row of three spinules at base of apical spine, not distinct at base, smooth, and about 0.8 times as long as endopod; endopod with apical spine reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 6O) also simple cuticular plate, but with inner distal corner more produced posteriorly and without (or with less) spinules along inner margin. Armature same as in male.

Sixth legs (Fig. 6O) vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material deposited in the copepod collection of the Arbeitsgruppe Zoomorphologie, University of Oldenburg, Germany (Coll. no. 1996.22/1–22/4 and 23/1–23/4).

TYPE LOCALITY: Spain, Cuenca Province, Salvacañete, River Cabriel at Los Hondonadas, spring at shore.

DISTRIBUTION: This species was collected in nine different locations in north-eastern Spain, from the Pyrenees to Valencia. Martínez Arbizu (1997) remarked that one of the rivers where this species was collected flows into the Atlantic in northern Portugal, which may suggest its wider westerly distribution.

ECOLOGY: Specimens were obtained from wells, hyporheic, and groundwater habitats, as well as from springs in riverbeds, in temperatures that ranged from 11 to 22°C, and in March, June, July, August, and September. This tells us about its wide ecological tolerance for many environmental factors, such as dissolved oxygen, temperature, water movement, and even water chemistry, and probably implies the absence of any seasonal dynamics. It can also be an indication of a species complex.

REMARKS: Martínez Arbizu (1997) assigned his new species to the *fontinalis* group and analysed the "phylogenetic relationships within the *fontinalis* group", but only considered five species and subspecies, although the "*fontinalis*" group contains more than 60 taxa (Karanovic, 2005a). The species is, however, an obvious member of the genus *Proserpinicaris*, considering the shape and armature of the fourth leg endopod in male, as well as the caudal rami armature. Not surprisingly, Martínez Arbizu (1997) found the phylogenetic position of this species to be quite isolated from other studied members of the *fontinalis* group! In our view, *P. hispanica* is relatively closely related to *P. proserpina*, *P. phyllura*, and even *P. cantabrica*, but can be distinguished by the proportions of the caudal rami and relative length of various armature elements on them, and to a lesser degree by details in the shape and armature of the fourth leg in male.

7. Proserpinicaris ima Cottarelli, 1989 (Fig. 7)

Parastenocaris ima Cottarelli, 1989, p. 286, figs. 1-3.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 306 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. No information available on somite ornamentation. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, reaching distal margin of first antennular segment, about as long as wide.

Anal somite (Fig. 7A, B) ornamented only with posterior row of small spinules laterally, and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with strongly convex and smooth distal margin, reaching beyond posterior end of anal somite, representing 50% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, one of on internal margin of anal operculum basally.

Caudal rami (Fig. 7A, B) about three times as long as greatest width (dorsal view) and about as long

as anal somite, mostly cylindrical, slightly divergent, with space between them about 1.5 times one ramus width, unornamented; armed with seven armature elements (three lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about 0.7 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other at 2/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.6 times as long as ramus, about four times and long as middle seta (minute), and 1.1 times as long as distalmost (ventralmost) one. Inner apical seta small, smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown. Outer apical seta also without breaking plane and relatively strong basally but much shorter, slightly longer than caudal ramus.

Antennula relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.3.6.3.0.0.8. All setae slender and all except largest seta on second segment smooth.

Antenna relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis partly divided, about 3.5 times as long as wide, unarmed, ornamented with two short rows of minute spinules on anterior surface. Endopod about 0.6 times as long as allobasis and 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single unipinnate apical seta, twice as long as segment.

Mandibula (Fig. 7C) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 7D) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 7E) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single smooth seta apically, distal endite armed with one smooth and one pinnate seta apically. Basis drawn out into strong pinnate claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with single smooth apical seta.

Maxilliped (Fig. 7F) with very short but strong syncoxa, unarmed and unornamented; basis slender, about four times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 7G) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on



Fig. 7. *Proserpinicaris ima*. Male: A. anal somite and left caudal ramus, lateral view; B. anal operculum and right caudal ramus, dosolateral view; C. mandibula; D. maxillula; E. maxilla; F. maxilliped; G. first swimming leg; H. second swimming leg; I. third swimming leg; J. fourth swimming leg; K. fifth leg. Female: L. second swimming leg without last two exopodal segments; M. third swimming leg; N. fourth swimming leg without last two exopodal segments; O. fifth leg. Scales: unknown (cited from Cottarelli, 1989, modified).

first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 7H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis probably unarmed (what appears to be a seta on Fig. 7H probably a large spinule), ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.1 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical, about five times as long as wide, reaching midlength of first exopodal segment, ornamented with several large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards (although leg twisted in Fig. 7H).

Third swimming leg (Fig. 7I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin; additional few spinules on anterior surface. Endopod absent. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with two small chitinous beaks on inner margin distally, ornamented with four large spinules on outer margin distally, armed subapically with spatulate, strong, and smooth spine, significantly longer than apophysis; ancestral distal segment (apophysis) cylindrical, oriented distally, unornamented and armed with single slender and smooth seta on top.

Fourth swimming leg (Fig. 7J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge curved chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long strong apical seta; apical seta 1.2 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, smooth, and from anterior view even more slender than spiniform process of basis.

Fifth leg (Fig. 7K) simple triangular cuticular plate, inner distal corner produced into long smooth spiniform process, ornamented with several spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; middle seta (ancestral outer endopodal) 0.35 times as long as leg, and 1.4 times as long as innermost seta. Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 292 μ m in paratype. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite. Other information on shape and ornamentation of somites missing.

Caudal rami very similar to male.

Antennula also seven-segmented but not geniculate, unornamented, with slender aesthetasc on

fourth segment, reaching slightly beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (probably incomplete): 0.3.6.1.0.0.7. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 7L), and exopod of fourth swimming leg (Fig. 2Q) similar to male.

Third swimming leg (Fig. 7M) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long smooth outer seta, longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, small, linguiform, ornamented with four spinules apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 7N) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, smooth, and about 0.7 times as long as endopod; endopod with apical spine reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 7O) also simple cuticular plate, but with inner distal corner more produced posteriorly and with single spinule on inner margin. Armature same as in male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: The holotype male and one paratype female were deposited in the Museo Civico di Storia Naturale "G. Doria" in Genova; the rest of the type material is deposited in the author's working collection in the Dipartimento di Scienze Ambientali, Università della Tuscia, Viterbo.

TYPE LOCALITY: Italy, Sardinia, Isola la Maddalena island, Casale Susini, artesian well 73 m deep, near the circum-island road.

DISTRIBUTION: This species is known only from the type locality, Isola la Maddalena island in Sardinia, Italy.

ECOLOGY: Specimens were obtained from a deep artesian well (73 m) on two separate occasions. This species is a proper stygobiont.

REMARKS: Cottarelli (1989) stated that *P. ima* is probably most similar morphologically to *P. admete*, which was described from several localities from Sardinia. He, however, maintained that there are enough morphological differences between the two to suggest separate specific statuses, most of them being present in the male third and fourth legs, as well as in the shape of the anal operculum and caudal rami in both sexes.

8. Proserpinicaris imjin Karanovic, Cho and Lee, 2012 (Figs. 8, 9)

Proserpinicaris imjin sp. nov. Karanovic et al. (2012).

Male: Total body length from 342 to 350 μ m. Colour, body segmentation, arthrodial membranes, and sensilla pattern as in *P. young* (see below). Habitus (Fig. 8A) cylindrical but not very slender,

without any demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width in dorsal view hard to establish. Body length/width ratio only about 7.2; cephalothorax about as wide as genital somite; free prosomites in lateral view about as wide as cephalothorax and not narrower than urosome, without any expansions laterally or dorsally. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes, except in preanal somite dorsally and partly laterally. Integument very weakly sclerotized, much softer than in *P. young* or in *P. wangpi* (see below), without any spinules or cuticular pits (except few spinules on caudal rami), but with slightly wrinkled surface, ornamentated as in other two Korean species with 45 pairs of sensilla and four pairs pores (three on anal somite, and one on caudal rami), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites, all in same position and of similar size as in *P. young* but not so well defined because of thin integument. Pleural areas of cephalothorax (Fig. 8A, B) and free pedigerous somites (Fig. 8C, D) not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view; rostrum and cuticular sutures of free pedigerous posomites as in *P. young*.

Cephalothorax (Fig. 8A, B) about 1.5 times as long as wide in dorsal view; representing 18% of total body length.

Urosomites (Fig. 8A) proportionately shorter and wider than in *P. young* or even *P. wangpi*, but without any difference in ornamentation. Anal somite (Figs. 8A, 9A, B) about as long as preanal somite, i.e. proportionately shorter than in other two species; anal operculum clearly concave in dorsal view.

Spermatophore (Fig. 9C) more slender than in *P. young*, about 2.4 times as long as wide.

Caudal rami (Figs. 8A, 9A, B) from 3.2 to 3.6 times as long as greatest width and only about as long as anal somite, cylindrical in anterior part but slightly inflated in posterior part in lateral view (arrowed in Fig. 9A), nearly parallel, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large lateral cuticular pore near posterior margin, and posterior ventral row of two small spinules. Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about as long as caudal ramus, triarticulate basally. Lateral setae slender and smooth, inserted very close to each other at 2/5 of ramus length, two larger ones more anteriorly and minute one in between and slightly more posteriorly. Anterior lateral seta which inserted more dorsally longest, 0.6 times as long as ramus, 1.3 times as long as other anterior seta, and about seven times as long as minute (distal) seta. Inner apical seta strongest, without breaking plane, unipinnate, about 1.5 times as long as ramus, pointing distally, with slightly curled tip. Outer apical seta also without breaking plane and unipinnate, relatively strong basally but much shorter, about 0.8 times as long as ramus, inserted close to dorsal surface and pointing laterally.

Antennula (Fig. 8B) relatively large, seven-segmented, prehensile and digeniculate, with distal part not clasped, fifth segment more robust than in *P. young*, armature and ornamentation without any difference, except aesthetasc on fifth segment narrowe and slightly shorter.

Antenna (Fig. 8B) more slender than in other two speices, with allobasis slightly more than four times as long as wide. Armature and ornamentation as in *P. young*.

Labrum (Fig. 8B), paragnaths (8A), mandibula (Fig. 8B), maxillula (Fig. 8A), maxilla (Fig. 8A), maxilliped (Fig. 8A), and first swimming leg (Fig. 8A) as in *P. young*.

Second swimming leg (Figs. 8A, 9D) as in *P. young*, except endopod not inflated in proximal half and about five times as long as wide and reaching 3/5 of first exopodal segment; apical seta 0.5 times as long as segment and pointing distally.



Fig. 8. *Proserpinicaris imjin*. Holotype male: A. habitus, lateral view; B. antennulae and antennae, lateral view; C. third and fourth swimming legs, lateral view; D. fifth and sixth legs, lateral view. Allotype female: E. prosome, lateral view; F. anal somite and caudal rami, dorsal view. Scales: $A=20 \ \mu m$, $B-F=10 \ \mu m$ (All SEM micrographs original).



Fig. 9. *Proserpinicaris imjin*. Paratype male: A. anal somite and right caudal ramus, lateral view; B. anal somite and caudal rami, ventral view; C. spermatophore; D. endopod of second swimming leg, anterior view; E. third swimming leg, posterior view. Paratype female: F. urosome, lateral view; G. last four antennular segments with incomplete armature, ventral view; H. endopod of second swimming leg, anterior view; I. third swimming leg, anterior view; J. endopod of third swimming leg, anterior view; K. endopod of fourth swimming leg, anterior view. Arrows pointing features different from other Korean short range endemics. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 50 μ m.

Third swimming leg (Figs. 8C, 9E) with tubular pore on posterior surface of first exopodal segment as in *P. wangpi* but general shape much more similar to that in *P. young*, except outer spine on first exopodal segment less robust and distal outer corner of proximal exopodal segment smooth (spinule missing). Leaf-like seta on apophysis smaller than in other two Korean species.

Fourth swimming leg (Fig. 8C) as in *P. young*, except apical seta on third exopodal segment somewhat shorter (about twice as long as third exopodal segment and 0.6 times as long as entire exopod); endopod and large basal spiniform process as in *P. young*, except also slightly short in proportion to first exopodal segment.

Fifth leg (Fig. 8D) simple triangular cuticular plate, inner distal corner produced into distally serrate spiniform process (which longer than in *P. young*), ornamented with four to six large spinules on inner margin, one arched proximal row of 14 minute spinules on posterior surface, and large cuticular pore on anterior surface; armature as in *P. young*, except inner endopodal seta only half as long as outer endopodal seta, and not reaching tip of distal spiniform process .

Sixth legs (Fig. 8D) smooth, unarmed and unornamented, forming simple operculum covering gonopore, slightly smaller than in *P. young*.

Female: Body length from 345 to 349 μ m. Habitus (Fig. 8E), ornamentation of prosomites, colour, and nauplius eye similar to male; genital and first abdominal somite fused into double somite and habitus less slender; free prosomites slightly narrower than urosomites in lateral view.

Genital double somite (Fig. 9F) slightly wider than long in dorsal view, without any trace of subdivision, with oval dorsal cuticular window in anterior half, which much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures covered by vestigial sixth legs; median copulatory pores also covered by fused sixth legs; seminal receptacles small, hard to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotized. All posterior senislla homologous to those on male third urosomite, while two sensilla from male second urosomite missing (Nos. 32 and 34).

Third (Fig. 9F), fourth (preanal) (Fig. 9F), and fifth (anal) (Figs. 8F, 9F) urosomites similar to male.

Caudal rami (Figs. 8F, 9F) laterally compressed but inflated in lateral view (arrowed in Fig. 9F), shorter in proportion to anal somite than in male, only about twice as long as wide. Apical armature in allotype much reduced in length, all less than half as long as caudal rami, but in paratypes not much different than in male (except outer apical seta slightly shorter). Lateral armature and ornamentation as in male.

Antennula (Figs. 8E, 9G) segmentation, ornamentation, and armature as in *P. young*, with both easthetascs very slender (i.e. much more slender than in *P. wangpi*).

Antenna (Fig. 8E), mandibula (Fig. 8E), maxillula (Fig. 8E), maxilla (Fig. 8E), maxilliped (Fig. 8E), first swimming leg (Fig. 8E), second swimming leg (Figs. 8E, 9H), and exopod of fourth swimming leg (Fig. 8E) similar to male.

Third swimming leg (Fig. 9I, J) as in *P. young*, but with shorter apical element on second exopodal segment, which even shorter than in *P. wangpi*.

Fourth swimming leg (Figs. 8E, 9K) without spiniform process on basis. Endopod one-segmented, straight, ornamented with apical row of two spinules at base of apical spine and three spinules on inner margin; apical spine not distinct at base, finely serrated (or bipinnate) distally, and about 0.8 times as long as endopod.

Fifth leg (Fig. 9F) also simple cuticular plate, but without any spinules along inner margin and with shorter distal spiniform process. Armature similar to male.

Sixth legs (Fig. 9F) vestigial, simple cuticular plates, covering gonopores, unornamented and

unarmed, completely fused, forming simple flap.

Type Locality: South Korea, Gyeonggido region, Paju city, Jeokseong town, Imjin River, interstitial, 37° 59'04.4"N 126° 55'41.2"E.

DISTRIBUTION: This species is only known from the type locality, the Imjin River near Jeokseong town (South Korea).

ECOLOGY: Specimens were obtained from the interstitial on the river banks, but no data are available on the water chemistry or sediment grain size.

SPECIMEN EXAMINED: Types only: holotype male and allotype female together on 1 SEM stub (collection number NIBRIV0000232626); one paratype male in alcohol (NIBRIV0000232627); four paratypes from a different sample (two males and two females) dissected on one slide each (collection numbers NIBRIV0000232628 to 0000232631); six paratypes from a different sample (four males and two females) together in alcohol (NIBRIV0000232632); all collected from the type locality, 14.vii.2010, leg. J.L. Cho, all deposited in the National Institute of Biological Resources, South Korea.

REMARKS: *Proserpinicaris imjin* is apparently very closely related to the Korean *P. ondali*, as well as to two other short-range endemics described by Karanovic et al. (2012): *P. wangpi* and *P. young* (see below). Their morphological differences are discussed in the remarks section of the latter species.

9. Proserpinicaris kalypso Pesce, Galassi and Cottarelli, 1988 (Fig. 10)

Parastenocaris kalypso Pesce et al., 1988, p. 138, figs. 16-31.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 375 to 454 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites as in female (Fig. 10I). Ornamentation of somites unknown.

Anal somite (Fig. 10A) ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with almost straight and smooth distal margin, not reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, three of which are on internal margin of anal operculum basally.

Caudal rami (Fig. 10A) about twice as long as greatest width (dorsal view) and almost 0.8 times as long as anal somite, inflated in anterior part and especially from lateral view, divergent, with space between them about 1.5 times one ramus width, unornamented; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about as long as caudal ramus, triarticulate basally. Lateral setae thin

and smooth, inserted close to each other but at 1/4 of ramus length. Proximalmost lateral seta placed more dorsally, 0.7 times as long as ramus, about three times and long as distal seta. Inner apical seta relatively large, inserted more ventrally, about as long as ramus. Middle apical seta strongest, without breaking plane, bipinnate, about 1.8 times as long as outer apical seta and 3.4 times as long as ramus. Outer apical seta also without breaking plane and bipinnate, relatively strong basally.

Antennula relatively long, seven-segmented, prehensile and digeniculate, but ornamentation and armature unknown.

Antenna (Fig. 10B) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis partly divided, about 3.5 times as long as wide, unarmed, ornamented with two short rows of large spinules on anterior surface. Endopod about 0.6 times as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula, maxillula, and maxilla unknown.

Maxilliped (Fig. 10C) with very short but strong syncoxa, unarmed and unornamented; basis slender, about four times as long as wide and several times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 10D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 10E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed and unornamented. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about 4.5 times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with two large spinules along apical margin and one on outer margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 10F) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin; additional few small spinules on anterior surface close to inner margin. Endopod absent. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with one large chitinous beak on inner margin at midlength, unornamented, armed subapically with complex, strong, smooth and curved spine, significantly longer than apophysis; ancestral distal



Fig. 10. *Proserpinicaris calypso*. Male: A. last four urosomal somites and left caudal ramus, lateral view; B. antenna; C. maxilliped; D. first swimming leg; E. second swimming leg; F. third swimming leg; G. fourth swimming leg; H. fifth leg. Female: I. urosome less fifth pedigerous somite, dorsal view; J. anal somite and caudal rami, dorsal view; K. antennula; L. second swimming leg without last two exopodal segments; M. third swimming leg; N. fourth swimming leg without last two exopodal segments; O. fifth leg. Scales: 50 μ m (cited from Pesce et al., 1988, modified).

segment (apophysis) small, conical, oriented slightly outwards, unornamented and unarmed, bilobate apically.

Fourth swimming leg (Fig. 10G) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with huge chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 1.1 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes proximally and smooth distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 10H) simple triangular cuticular plate, inner distal corner produced into long and smooth spiniform process, ornamented with several large spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.1 times as long as entire leg; middle seta (ancestral outer endopodal) 0.45 times as long as leg, and only slightly longer than innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 400 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite and habitus slightly less slender.

Genital double somite (Fig. 10I) slightly wider than long (dorsal view; although probably compressed), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex unknown. Third, fourth (preanal), and fifth (anal) (Fig. 10J) urosomal somites similar to male.

Caudal rami (Fig. 21J) much more slender than in male, but armature very similar.

Antennula (Fig. 10K) also seven-segmented but not geniculate, unornamented, with slender aesthetasc on fourth segment, reaching tip of appendage, and probably with more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (certainly incomplete): 0.2.2.2.0.0.6. All setae smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 10L), and exopod of fourth swimming leg (Fig. 10N) similar to male.

Third swimming leg (Fig. 10M) with large praecoxa, smooth coxa and intercoxal sclerite. Basis unornamented but armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with single spinule apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 10N) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, and about 0.9 times as long as endopod; endopod with apical spine reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 10O) also simple cuticular plate, but more slender, and without spinules along

inner margin. Armature same as in male, except middle seta slightly longer.

Sixth legs unknown nut probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: One paratype male deposited in the Zoological Museum of the University of Amsterdam (ZMA Co. 102.808). Other type material was deposited in the senior author's working collection (University of l'Aquila) and destroyed during the 2009 earthquake.

TYPE LOCALITY: Italy, Sicily, Petrosino near Trapani, freshwater well.

DISTRIBUTION: This species is known only from the type locality, a freshwater well in Petrosino near Trapany, Sicily, Italy.

ECOLOGY: Specimens were obtained from a freshwater well only, so very little is known about this species' ecology. Pesce et al. (1988) reported that the water table was 14.5 m from the surface, and the depth of water in the well was 2.5 m. Other environmental conditions recorded at the time of sampling include temperature (20°C), pH (6.8), and the type of bottom (clay and sandstone). It is possible that the species is restricted to the layer of sandstone sediment on this part of the island. It was found sympatrically with another, not closely related parastenocarid: *Parastenocaris trinacriae* Pesce, Galassi and Cottarelli, 1988.

REMARKS: Pesce et al. (1988) noted that *P. kalypso* is probably most similar morphologically to *P. proserpina*, which lives in central parts of continental Italy. The main differences include fine details in shape and ornamentation of the male third and fourth legs, which are sexually dimorphic characters. They also pointed some similarities with *P. ruffoi* Chappuis, 1955, but noted a completely different caudal rami morphology.

10. *Proserpinicaris mangini* Rouch, 1992 (Fig. 11)

Parastenocaris mangini Rouch, 1992, p. 306, figs. 1-3.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 358 μ m. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Ornamentation of somites and presence/absence of cuticular windows unknown.

Anal somite (Fig. 11A, B) ornamented only with several spinules ventrally at base of caudal rami, and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, reaching beyond posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 11A, B) almost four times as long as greatest width (dorsal view) and about as long as anal somite, cylindrical but slightly tapering posteriorly, parallel, with space between them about 1.5 ramus width; armed with seven armature elements (three lateral, one dorsal, and three

apical). Ornamentation consists of few ventral spinules on posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about 0.65 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other at midlength of ramus. Proximal lateral seta placed more dorsally, 0.3 times as long as ramus, and more than twice as long as other two lateral setae, which are subequal. Inner apical seta slender and smooth, inserted more ventrally, about 0.7 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown. Outer apical seta also without breaking plane and smooth, relatively strong basally, but much more slender and shorter, only about 0.7 times as long as caudal ramus.

Antennula (Fig. 11C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender and short aesthetasc on fourth segment not reaching tip of appendage, fused basally to slightly longer seta. Not much shorter apical aesthetasc on seventh segment, fused basally to at least one seta. Setal formula: 0.6.4.5.1.0.7. All setae slender and smooth.

Antenna (Fig. 11D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed but ornamented with two large spinules proximally on anterior surface. Endopod about 0.6 times as long as allobasis and 2.2 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula (Fig. 11E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 11F) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 11G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with two setae apically. Basis drawn out into strong and pinnate claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 11H) with very short syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and five times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.9 times as long as basis.

First swimming leg (Fig. 11I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times

as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.25 times as long as entire endopod and as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 11J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about six times as long as wide, reaching slightly beyond midlength of first exopodal segment in length, ornamented with four large spinules along apical margin and one on outer margin; armed apically with one smooth seta, about as long as segment and pointing distally.

Third swimming leg (Fig. 11K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta, ornamented with diagonal row of large spinules close to outer margin. Endopod minute, spiniform, about as long as spinules on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment 3.5 times as long as wide, oriented inwards, with small beak on inner margin proximally, ornamented with tubular pore on inner margin at base of cuticular beak and with long row of large spinules on outer margin, armed subapically with simple, strong, smooth and sharp spine, as long as apophysis with armature; ancestral distal segment (apophysis) thumb-like, very short, unornamented but armed with single slender and smooth seta on top.

Fourth swimming leg (Fig. 11L) with smooth praecoxa and intercoxal sclerite. Coxa unarmed, ornamented with bunch of spinules on inner margin. Basis armed with single outer seta, ornamented with large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, slightly longer and much stronger than basal spiniform process, elaborately decorated with serrulate membranes and tubercules, reaching midlength of first exopodal segment in length.

Fifth leg (Fig. 11M) simple triangular cuticular plate, three times as long as wide, inner distal corner produced into short and smooth spiniform process, ornamented with large spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, 0.7 times as long as entire leg; middle seta (ancestral outer endopodal) only 0.2 times as long as leg, and 1.4 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 347 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender. Caudal rami very similar to male.

Antennula (Fig. 11N) also seven-segmented but not geniculate, with slender aesthetasc on fourth segment, not reaching tip of appendage, and much shorter apical aesthetasc on seventh segment, fused basally to at least one apical seta; both aesthetascs equally slender as in male; setal formula



Fig. 11. *Proserpinicaris mangini*. Male: A. anal somite and left caudal ramus, dorsal view; B. anal somite and right caudal ramus, lateral view; C. antennula; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. fourth swimming leg; M. fifth leg. Female: N. distal part of antennula; O. third swimming leg; P. fourth swimming leg without last two exopodal segments; Q. fifth leg. Scales: 30 μ m (cited from Rouch, 1992, modified).

(possibly incorrect): 0.4.4.2.1.0.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming, and exopod of fourth swimming leg (Fig. 11P) similar to male.

Third swimming leg (Fig. 11O) with large praecoxa, smooth coxa and intercoxal sclerite. Basis unornamented, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, unarmed and unornamented, reaching only 1/5 of first exopodal segment in length.

Fourth swimming leg (Fig. 11P) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, smooth, and about 0.8 times as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 11Q) also simple cuticular plate, but somewhat wider and without spinules along inner margin, instead ornamented with several spinules at base of spiniform process. Armature same as in male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: France, Ariège, Baget karst system, Gouffre de la Peyrère, cave.

DISTRIBUTION: This species is known only from the type locality, Gouffre de la Peyrère in Ariège, France.

ECOLOGY: The specimens were collected along with a rich stygofauna, consisting of 51 species of crustaceans (22 of them copepods), from a submerged subterranean lake in the Baget karst system. This locality is one of the principal recharge points of the whole system, so it can be expected to be an important place of surface-carbon influx, and thus a prime habitat for stygofauna. Little is known about the environmental conditions and precise habitat of this species though. Rouch (1992) only stated that all specimens were collected with a fine plankton net, so we presume that *P. mangini* Rouch, 1992 was collected directly from the water column or (more probably) from the benthic and suprabenthic habitat.

REMARKS: Rouch (1992) assigned his new species to the *proserpina* group, considering the shape and armature of the fourth leg endopod in male, as well as the caudal rami armature. He compared his species with 14 known members of this group, known to him at that time, but considered the combination of the third leg shape and armature in male, along with that of the fourth leg and caudal rami, to be unique.

11. Proserpinicaris meridionalis Rouch, 1990 (Fig. 12)

Parastenocaris fontinalis meridionalis Rouch, 1990, p. 23, figs. 3–5. *Parastenocaris meridionalis* (Rouch): Martínez Arbizu, 1997, p. 223.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (exclud-

ing caudal setae), 431 μ m in holotype. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules except on anal somite). Presence of cuticular windows, shape and detailed ornamentation of cephalothorax and free somites, and rostrum unkown.

Anal somite (Fig. 12A, B) about as long as wide, ornamented with seven spinules at base of each caudal ramus and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 65% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 12A, B) about three times as long as greatest width (ventral view) and about as long as anal somite, mostly cylindrical but slightly tappering posteriorly, divergent, with space between them about 1.3 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation not reported. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about 0.8 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 2/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.4 times as long as ramus, about five times as long as two other minute setae. Inner apical seta slender and smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 2.5 times as long as outer apical seta or caudal ramus, pointing distally but with distal tip curved outward. Outer apical seta also without breaking plane and smooth, relatively strong basally, pointing disto-laterally.

Antennula (Fig. 12C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Wide aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly shorter seta. Slightly shorter but equally robust apical aesthetasc on seventh segment, also fused basally to slightly shorter seta. Setal formula (probably incomplete): 0.6.5.5.0.1.7. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 12D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unarmed and unornamented. Allobasis about 2.7 times as long as wide, unarmed, ornamented at least with single large spinules on anterior surface proximally. Endopod about 0.8 times as long as allobasis and 2.7 times as long as wide, with surface frill subdistally, ornamented with two rows of large spinules on anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about three times as long as wide, unornamented but armed with single apical seta, which twice as long as segment.

Mandibula (Fig. 12E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 12F) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as

wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 12G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 12H) with very short syncoxa, unarmed and unornamented; basis slender, nearly four times as long as wide and nearly six times as long as syncoxa, unornamented and unarmed; endopod represented by long claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, neary 0.9 times as long as basis.

First swimming leg (Fig. 12I) with smooth praecoxa, coxa and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with row of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about three times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long spinule on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.4 times as long as entire endopod, 3.5 times as long as outer spine, and about as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 12J) also with smooth praecoxa, coxa and intercoxal sclerite. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one slightly longer than exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and short, about 3.7 times as long as wide, reaching midlength of first exopodal segment in length, ornamented with four large spinules along apical margin and two on outer margin; armed apically with one smooth and short seta, only about half as long as segment and pointing distally.

Third swimming leg (Fig. 12K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod minute, spiniform, about as long as spinules on outer margin, inserted at about 2/5 of basis length. Exopod with both segments fused; ancestral proximal segment three times as long as wide, curved inwards and with two large chitinous beaks on inner margin proximally, ornamented with seven large spinules on outer margin proximally and tube pore on inner margin, armed subapically with simple, strong, smooth and distally flattened spine, significantly longer than apophysis; ancestral distal segment (apophysis) cylindical, oriented distally, unornamented and armed with single very short and smooth spine on top.

Fourth swimming leg (Fig. 12L) with smooth praecoxa and intercoxal sclerite. Coxa unarmed, ornamented with bunch of spinules on inner margin. Basis armed with single outer seta, ornamented with diagonal row of few spinules near outer margin and small chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer



Fig. 12. *Proserpinicaris meridionalis*. Male: A. anal somite and caudal rami, dorsal view; B. anal somite and right caudal ramus, ventral view; C. antennule; D. antenna; E. mandibular; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. fourth swimming leg; M. fifth leg. Female: N. antennule; O. third swimming leg; P. fourth swimming leg; Q. fifth leg. Scales: 30 μ m (cited from Rouch, 1990, modified).

margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine, and additionally ornamented with two enlarged spinules on inner margin distally; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and about 2.6 times as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membrane distally along outer margin, resembling some primitive, Stone-Age spear tip; ornamented with two spinules at about first quarter of endopod's length.

Fifth leg (Fig. 12M) simple but large triangular cuticular plate, 3.6 times as long as wide, inner distal corner produced into short and smooth spiniform process, ornamented with several spinules along inner margin at first third of its length, armed with four smooth setae; outermost seta (ancestral basal one) longest, 0.6 times as long as entire leg; next seta (ancestral exopodal) much smaller, 0.1 times as long as outermost seta and inserted close to it; third seta (ancestral outer endopodal) 0.14 times as long as leg, and 1.1 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 380 μ m. Habitus, caudal rami, ornamentation of somites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Antennula (Fig. 12N) also seven-segmented but not geniculate, with slender aesthetasc on fourth segment, reaching midlength of seventh segment in length, and more slender and much shorter apical aesthetasc on seventh segment; both aesthetascs much more slender than in male; setal formula (possibly incoplete): 0.5.3.1.1.0.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 12O) similar to male.

Third swimming leg (Fig. 12P) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with long and smooth outer seta, which slightly shorter than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with few spinules apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 12O) without spiniform process on basis. Endopod one-segmented, ornamented with two spinules on inner (?) margin and transverse apical row of three spinules at base of apical spine, not distinct at base, smooth, and about 0.7 times as long as endopod; endopod (together with apical spine) reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 12Q) also simple cuticular plate, but with inner distal corner slightly shorter and without spinules along inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: France, Ariège, commune d'Encourtiech, Ruisseau le Nert, interstitial waters.

DISTRIBUTION: This species is only known from the type locality, interstitial waters at Ruisseau le Nert, in the south of France. It is probably a short range enemic.

ECOLOGY: Specimens were obtained by pumping from interstitial sediments. The species is probably a stygobiont.

REMARKS: Martínez Arbizu (1997) elevated this subspecies to the full specific rank, while describing a relatively closely related new species from Spain (*P. hispanica*). Unfortunately, he assigned both species to the *fontinalis* group and analysed the "phylogenetic relationships within the *fontinalis* group", but only considered five species and subspecies, although the *fontinalis* group contains more than 60 taxa. Karanovic (2005a) pointed out that both are members of the *proserpina* group, and Karanovic et al. (2012) formally transferred them into the redefined genus *Proserpinicaris*, considering the shape and armature of the fourth leg endopod in male, as well as the caudal rami armature. *Proserpinicaris meridionalis* differes from *P. hispanica* in the shape of the male third leg, size of the smallest seta on the fifth leg in both sexes, as well as number and size of the inner spinules on the male fourth leg exopod. In our view, *P. meridionalis* is also relatively closely related to *P. proserpina, P. phyllura* and even *P. cantabrica*, but can be distinguished by the proportions of the caudal rami and relative length of various armature elements on them, and, to a lesser degree, by details in the shape and armature of the fourth leg in male. Differences from *P. fontinalis* are too numerous to list and include absence of a hyaline process on the fourth leg basis in male.

12. Proserpinicaris moravica Šterba, 1965 (Fig. 13)

Parastenocaris moravica Šterba, 1965, p. 204, figs. 1-10.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 400 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus not known, but judging from drawings of anal somite probably cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by welldeveloped arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules). Information about cuticular windows missing.

Anal somite (Fig. 13A) probably ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with strongly convex and smooth distal margin, reaching beyond posterior end of anal somite, representing 55% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 13A) about four times as long as greatest width and almost 0.7 times as long as anal somite, unornamented, almost cylindrical and parallel, with space between them about one ramus width; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6, about 0.6 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at midlength. Proximalmost lateral seta placed more dorsally, 0.7 times as long as ramus, and about four times and long as other seta (minute). Inner apical seta small, smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth,

length unknown. Outer apical seta also without breaking plane but much smaller, about as long as dorsal seta.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped not described, but presumably similar to those in type species.

First swimming leg similar to that in female (Fig. 13F) with smooth praecoxa, coxa, and intercoxal sclerite. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.8 times as long as entire endopod, and almost 1.5 times as long as larger geniculate exopodal seta.

Second swimming leg similar to that in female (Fig. 13G) with smooth praecoxa, coxa, intercoxal sclerite, and basis. Basis unarmed. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about eight times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with several large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 13B) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod probably absent. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with smooth inner margin distally, ornamented with several spinules on outer margin proximally, armed subapically with complex, strong, smooth and curved spine, about as long as apophysis; ancestral distal segment (apophysis) conical, oriented slightly inwards, unornamented and armed with single smooth seta on top.

Fourth swimming leg (Fig. 13C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with huge chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with convex inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and more than four times as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes proximally and distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 13D) simple triangular cuticular plate, inner distal corner produced into short smooth spiniform process, ornamented with several spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; middle seta (ancestral outer endopodal) much shorter, 0.3 times as long as leg, and 1.2 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 500 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double



Fig. 13. *Proserpinicaris moravica*. Male: A. anal somite and left caudal ramus, lateral view; B. third swimming leg; C. fourth swimming leg; D. fifth leg. Female: E. anal somite and caudal rami, dorsal view; F. first swimming leg; G. second swimming leg; H. third swimming leg; I. fourth swimming leg; J. fifth legs. Scales: unknown (cited from Šterba, 1965, modified).

somite and habitus slightly less slender.

Anal somite and caudal rami (Fig. 13E) very similar to male, ramus only slightly shorter in proportion to anal somite and with somewhat longer proximal lateral seta.

Antennula unknown.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 13F), second swimming leg (Fig. 13G), and exopod of fourth swimming leg (Fig. 13I) similar to male.

Third swimming leg (Fig. 13H) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with short outer seta. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with three spinules apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 13I) without spiniform process on basis. Endopod one-segmented, ornamented with several spinules at base of apical spine, indistinct at base, bipinnate, and about as

long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 13J) also simple cuticular plate, but more elongated and without spinules along inner margin. Armature similar as in male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: Not specified. Species described simultaneously from five different localities in Slovakia.

DISTRIBUTION: This species was described from five different localities from four rivers and creeks in central, north, and east Slovakia: Třebůvka creek near Bouzov; Třebůvka creek near Kozov, Morava river near Stren, Opava creek near Albrechtice, and Bečva creek near Horní Bečva.

ECOLOGY: This is a very characteristic interstitial species, all samples being taken from sandy banks of rivers and creeks using the Karaman-Chappuis method.

REMARKS: Sterba (1965) noted a close morphological similarity of this species to *P. proserpina*, but he also listed two other completely unrelated species as close relatives. We, however, agree with him that the caudal rami shape and armature distinguish *P. moravica* from *P. proserpina*, as well as from any other member of this group. The shape of the fourth leg in the male is very similar to those of other members of the genus *Proserpinicaris*. The third leg in male is also very characteristic in this species.

13. Proserpinicaris nicolasi Rouch, 1996 (Fig. 14)

Parastenocaris nicolasi Rouch, 1996, p. 41, figs. 1-3.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 456 μ m. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Ornamentation of somites and presence/absence of cuticular windows unknown.

Anal somite (Fig. 14A, B) ornamented only with several spinules ventrally at base of caudal rami, another row of spinules dorsolaterally along posterior margin, and with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with concave and smooth distal margin, reaching posterior end of anal somite, representing 75% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 14A, B) about three times as long as greatest width (lateral view) and almost 0.8 times as long as anal somite, mostly cylindrical but slightly inflated posteriorly, slightly divergent, with space between them about one ramus width; armed with six armature elements (two lateral,

one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally. Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about 0.8 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other at 1/3 of ramus length. Proximal lateral seta placed more dorsally, 0.6 times as long as ramus, and 3.2 times as long as distal seta. Inner apical seta small, smooth, inserted more ventrally, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown. Outer apical seta also without breaking plane and smooth, relatively strong basally, much more slender and shorter, only about as long as caudal ramus.

Antennula (Fig. 27C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender and short aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Even shorter apical aesthetasc on seventh segment, fused basally to at least one seta. Setal formula: 0.6.3.6.0.0.7. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 14D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed and unornamented. Endopod about 0.6 times as long as allobasis and 2.2 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical unipinnate seta, twice as long as segment.

Mandibula (Fig. 14E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 14F) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with strong lateral seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 14G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single smooth seta apically, distal armed with two setae apically. Basis drawn out into strong pinnate claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 14H) with very short syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and seven times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.9 times as long as basis.

First swimming leg (Fig. 14I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on posterior margin at base of endopod, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal
margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.1 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 14J) with smooth praecoxa, and intercoxal sclerite. Coxa with row of minute spinules on outer margin, unarmed. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one almost as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about five times as long as wide, reaching slightly beyond midlength of first exopodal segment in length, ornamented with four large spinules along apical margin and one on outer margin; armed apically with one smooth seta, about half as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 14K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis extremely large, almost twice as long as praecoxa and coxa combined, robust, armed with long outer seta, ornamented with diagonal row of large spinules close to outer margin, and additional longitudinal row of spinules along inner margin proximally. Endopod minute, spiniform, about twice as long as spinules on outer margin and stronger, unornamented. Exopod with both segments fused; ancestral proximal segment three times as long as wide, oriented dorsally, with concave inner margin, unornamented, armed subapically with simple, strong, smooth and blunt spine, as long as apophysis; ancestral distal segment (apophysis) thumb-like, wider than first exopodal segment, unornamented and armed with single short and smooth seta on top.

Fourth swimming leg (Fig. 14L) with smooth praecoxa and intercoxal sclerite. Coxa unarmed, ornamented with bunch of spinules on inner margin. Basis armed with single outer seta, ornamented with two large spinules near outer margin and large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.9 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and complex, inflated inwards basally, elaborately decorated with serrulate membranes proximally on inner side and distally on outer side, about as wide as first exopodal segment and reaching its distal margin in length.

Fifth leg (Fig. 14M) simple triangular cuticular plate, four times as long as wide, inner distal corner produced into short and smooth spiniform process, ornamented with large spinules along inner margin, armed with four smooth setae; outermost seta (ancestral basal one) longest, 0.9 times as long as entire leg; next seta (ancestral exopodal) minute, smaller than spinules on inner margin; third seta (ancestral outer endopodal) 0.34 times as long as leg, and 1.2 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 448 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender. Caudal rami very similar to male.

Antennula (Fig. 14N) also seven-segmented but not geniculate, with slender aesthetasc on fourth



Fig. 14. *Proserpinicaris nicolasi*. Male: A. anal somite and left caudal ramus, lateral view; B. caudal part of anal somite and right caudal ramus, dorsal view; C. antennula; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. fourth swimming leg; M. fifth leg. Female: N. distal part of antennula; O. third swimming leg; P. fourth swimming leg without last two exopodal segments; Q. fifth leg. Scales: 30 μ m (cited from Rouch, 1996, modified).

segment, reaching tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to at least one apical seta; both aesthetascs equally slender as in male; setal formula (possibly incorrect): 0.4.4.2.0.1.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 14P) similar to male.

Third swimming leg (Fig. 14O) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with two spinules apically, unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 14P) without spiniform process on basis. Endopod one-segmented, ornamented with several spinules on outer margin and transverse apical row of three spinules at base of apical spine, not distinct at base, smooth, and about 0.7 times as long as endopod; endopod with apical spine reaching slightly beyond posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 14Q) also simple cuticular plate, but somewhat wider and without spinules along inner margin. Armature same as in male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: France, Haute-Garonne region, Fronton village, Verdure creek (part of the River Tarn drainage area), interstitial.

DISTRIBUTION: This species is known only from the type locality, interstitial near Fronton village, France.

ECOLOGY: Little is known about the environmental conditions and habitat of this species. Rouch (1996) only stated that the specimens were collected with a pump, some 10 m from the creek, but we know nothing about the sediments, depth from which the specimens came or water temperature for example.

REMARKS: Rouch (1996) assigned his new species to the *proserpina* group, considering the shape and armature of the fourth leg endopod in male, as well as the caudal rami armature. He listed 12 known members of this group, known to him at that time, considering his species most closely related to *P. proserpina*, *P. admete*, *P. moravica*, and *P. mangini*. From all four, however, *P. nicolasi* differs by the shape of the fourth leg endopod in male, inflated in proximal part. We should add here also an unusually long basis of the third leg in male, a unique character in the entire family.

14. Proserpinicaris nipponensis Chappuis, 1955 (Fig. 15)

Parastenocaris nipponensis Chappuis, 1955, p. 187, figs. 23–29; Miura, 1964, p. 140, figs. 45–54. *Parastenocaris nipponica* Chapp.: Chappuis, 1958, p. 429, fig. 12. [non] *Parastenocaris nipponensis* Chappuis: Miura, 1969, p. 253, figs. 45–51.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 400 to 450 μ m. Preserved specimen white. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Ornamentation of somites and presence/absence of cuticular windows unknown.

Anal somite (Fig. 15A, B) ornamented with pair of large dorsal sensilla at base of anal operculum, two short transverse ventral rows of spinules at first third, and with several minute spinules along posterior margin ventrally, at base of caudal rami. Anal operculum well developed, unornamented on outer surface, with concave distal margin between produced lateral corner, almost reaching posterior end of anal somite, representing 85% of somite width. Anal sinus widely opened and smooth.

Caudal rami (Fig. 15A, B) about five times as long as greatest width (dorsal view) and about 1.25 times as long as anal somite, cylindrical and only tapering posteriorly in last sixth, divergent, with space between them about 2.5 ramus width; armed with six armature elements (two lateral, one dorsal, and three apical). Ornamentation consists of few ventral spinules on posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6, about 0.4 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other at about 2/3 of ramus length, almost equal in length. Inner apical seta slender and smooth, inserted more ventrally, about 0.45 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown but much longer than caudal ramus. Outer apical seta relatively small and slender, only about as long as lateral setae.

Antennula relatively long, seven-segmented, prehensile and digeniculate, unornamented. Armature unknown.

Antenna, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown but probably similar to type species.

Second swimming leg with smooth praecoxa, coxa, and intercoxal sclerite. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical ornamented with several spinules along apical margin; armed apically with one smooth seta.

Third swimming leg (Fig. 15C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta, unornamented. Endopod reduced to slender seta, about half the length of basis, unornamented. Exopod with both segments fused; ancestral proximal segment about three times as long as wide, oriented inwards, with small beak on inner margin proximally, but with slightly concave inner margin, ornamented with three spinules on outer margin, armed subapically with simple, strong, smooth and sharp spine, somewhat longer than apophysis, and pointing distally; ancestral distal segment (apophysis) thumb-like, relatively short, unornamented and unarmed, with inner distal corner produced into spiniform process (probably fused ancestral apical spine).

Fourth swimming leg (Fig. 15D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with large chitinous inwards-pointing spiniform process between exopod and endopod.

Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta almost as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, much shorter than basal spiniform process, ornamented with one or two short spinules on outer margin, curved and pointing outwards.

Fifth leg (Fig. 15E) simple triangular cuticular plate, sharply pointed in distal half, 4.3 times as long as wide, inner distal corner produced into sharp and smooth spiniform process, unornamented, armed with three smooth setae; outermost seta (ancestral basal one) longest, half as long as entire leg; middle seta (ancestral outer endopodal) smallest, 0.3 times as long as basal seta, and half as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 450 to 470 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite (Fig. 15H) and habitus slightly less slender. Caudal rami (Fig. 15F, G) very similar to male, but slightly more elongated, and with slightly longer proximal lateral seta and shorter innermost apical one, although this may be the result of intraspecific variability rather than sexual dimorphism.

Antennula (Fig. 15I) also seven-segmented but not geniculate, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and somewhat shorter apical aesthetasc on seventh segment, fused basally to at least one apical seta; setal formula (certainly incomplete): 0.0.4.1.0.0.5.

Antenna (Fig. 15J) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed but ornamented with two large spinules proximally on anterior surface. Endopod half as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula, maxillula, maxilla, maxilliped, exopod of fourth swimming leg (Fig. 15N) similar to male.

First swimming leg (Fig. 15K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 15L) with smooth praecoxa, coxa, and intercoxal sclerite. Basis also unarmed and unornamented. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (pro-



Fig. 15. *Proserpinicaris nipponensis*. Male: A. anal somite and right caudal ramus, ventral view; B. anal somite and right caudal ramus, dorsal view; C. third swimming leg; D. fourth swimming leg without last two exopodal segments; E. fifth leg. Female: F. anal somite and caudal rami, dorsal view; G. anal somite and right caudal ramus, ventral view; H. fifth pedigerous somite with fifth legs and genital double somite, ventral view; I. antennula; J. antenna; K. first swimming leg; L. second swimming leg; M. third swimming leg; N. fourth swimming leg; O. fifth leg. Scales: unknown (cited from Chappuis, 1955 and Miura, 1964, modified).

bably outer spine and two apical setae), innermost one as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about five times as long as wide, reaching slightly beyond midlength of first exopodal segment in length, ornamented with four large spinules along apical margin; armed apically with one smooth and short, less than half as long as segment and pointing slightly outwards (although probably segment was twisted during slide preparation).

Third swimming leg (Fig. 15M) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with few spinules on outer margin, armed with very long and smooth outer seta. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, spiniform, unarmed and unornamented, reaching midlength of first exopodal segment.

Fourth swimming leg (Fig. 15N) without spiniform process on basis. Endopod one-segmented, spiniform, unornamented, armed with bipinnate apical spine, fused at base, smooth, about as long as endopod; endopod with apical spine reaching slightly beyond posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 15O) also simple cuticular plate, but somewhat more elongated in distal part, also without spinules along inner margin. Armature same as in male, but distance between basal seta and two endopodal setae shorter.

Sixth legs (Fig. 15H) vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single flap.

TYPE: Type material probably lost.

TYPE LOCALITY: Japan, Honshu Island, Hyogo Prefecture, Aioi village near Himeji town, village water-supply well.

DISTRIBUTION: This species is only known from the type locality, a well in Aioi, Hyogo Prefecture, Japan, where it was collected on at least two occasions (Chappuis, 1955; Miura, 1964).

ECOLOGY: Little is known about the environmental conditions where this species lives. It was collected at least twice from the same well, which was part of the water-supply system of a small village. This means that the water was probably constantly pumped out. Thus, the habitat for *P. niponnensis* must be the surrounding interstitial in alluvial sediments. We do not know, however, the exact location of this well.

REMARKS: Chappuis (1955) did not discuss the affinities of his new species, as in many other papers. Subsequently he (Chappuis, 1958) did include it in a key to species on page 430, and provided a repeated drawing of the male fourth swimming leg (Fig. 12), although in the Fig. legends he erroneously spelled the species name as *P. nipponica* Chapp. (see synonymy section above). Miura (1964) redescribed the species from freshly collected material (presumably from the type locality), but also did not comment on its affinities. A few years later, Miura (1969) reported this species from South Korea, also without comments and with a few additional drawings. It is quite clear from those drawings that Miura (1969) did not find *P. nipponensis* in South Korea but a new species, although relatively closely related. This species was described as new recently by Lee and Chang (2009), who also synonymised Miura's *P. nipponensis* for the first time. Karanovic et al. (2012), however, synonymized Miura's Korean record with their new species *P. wangpi* (see below).

15. Proserpinicaris ondali Lee and Chang, 2009 (Fig. 16)

Parastenocaris ondali Lee and Chang, 2009, p. 170, figs. 2–5; Chang, 2010, p. 94, fig. 42. [non] *Parastenocaris nipponensis* Chappuis: Miura, 1969, p. 253, figs. 47–51.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 430 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 16A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about 9.2; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax (Fig. 16A) about 1.8 times as long as wide in dorsal view; representing 19% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally relatively simple, with eight large sensilla surrounding dorsal cuticular window.

Urosomal somites (except preanal, unornamented) with eight posterior sensilla and with smooth hyaline fringes.

Anal somite (Fig. 16A) ornamented with pair of large dorsal sensilla at base of anal operculum, ventral pore at base of caudal rami, and two short rows of spinules on ventral surface at anterior third. Anal operculum well developed, unornamented on outer surface, with almost straight and smooth distal margin, almost reaching posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened, ornamented with numerous minute and slender spinules.

Caudal rami (Fig. 16A) almost five times as long as greatest width (dorsal view) and about as long as anal somite, cylindrical, divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally, and posterior row of several spinules ventrally. Dorsal seta slender and smooth, inserted closer to inner margin at about 4/5, about as long as caudal ramus, triarticulate basally. Lateral setae slender and smooth, inserted close to each other but at midlength. Proximalmost lateral seta placed more dorsally, 0.6 times as long as ramus, about seven times and long as middle seta (minute), and 1.3 times as long as ramus. Middle apical seta strongest, without breaking plane, unipinnate, about four times as long as ramus. Outer apical seta also without breaking plane and unipinnate, relatively strong basally but much shorter, about as long as ramus.

Antennula (Fig. 16B) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process, but small spiniform process present on fourth segment proximally. Massive aesthetasc on fourth segment reaching tip of appendage, fused basally to slightly longer seta. Much shorter and more slender apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (possibly incomplete): 0.6.4.4.0.0.6. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 16C) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about four times as long as wide, unarmed but ornamented with two large spinules proximally on anterior surface. Endopod half as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula (Fig. 16D) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 16E) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 16F) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong pinnate claw, probably without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 16J) with short and relatively strong syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and as many times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, ornamented with several spinules along concave margin distally, about 0.8 times as long as basis.

First swimming leg (Fig. 16H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on posterior margin between endopod and endopod, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 16I) with smooth praecoxa, and intercoxal sclerite. Coxa with diagonal row of minute spinules on anterior surface. Basis unarmed, ornamented with row of spinules on



Fig. 16. *Proserpinicaris ondali*. Male: A. habitus, dorsal view; B. antennula; C. antenna; D. mandibula; E. maxillula; F. maxilla; G. maxilliped; H. first swimming leg; I. second swimming leg; J. third swimming leg; K. fourth swimming leg; L. fifth leg. Female: M. anal somite and caudal rami, ventral view; N. anal somite and left caudal ramus, lateral view; O. antennula; P. basis and first endopodal and exopodal segments of first swimming leg; Q. third swimming leg; R. fourth swimming leg; S. fifth leg. Scales: 50 μ m (cited from Lee and Chang, 2009 and Chang, 2010, modified).

outer margin and few spinules at base of endopod. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.1 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, almost five times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with few large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 16J) with smooth praecoxa and intercoxal sclerite. Coxa with arched row of large spinules on anterior surface. Basis robust, unornamented, armed with outer long and slender seta. Endopod minute but distinct segment, curved, about twice as long as largest spinule on coxa, unornamented. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with small chitinous bulge on inner margin distally, unornamented, armed subapically with simple, strong, smooth and inward curved spine, longer than apophysis; ancestral distal segment (apophysis) conical, oriented slightly inwards, unornamented and armed with single short, leaf-like seta on top.

Fourth swimming leg (Fig. 16K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with huge, inwards-pointing chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, additionally ornamented with long and slender spinule on inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.7 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but with apical crown of spinules.

Fifth leg (Fig. 16L) simple triangular cuticular plate, inner distal corner produced into long and smooth spiniform process, ornamented with several spinules along inner margin, several more minute spinule on posterior surface proximally, and cuticular pore on anterior surface, armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.2 times as long as entire leg; middle seta (ancestral outer endopodal) smallest, 0.2 times as long as leg, and half as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 450 to 510 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite slightly longer than wide (dorsal view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores also covered by fused sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami (Fig. 16M, N) very similar to male, and only slightly shorter in lateral view.

Antennula (Fig. 16O) also seven-segmented and unornamented but not geniculate, with slender aesthetasc on fourth segment, not reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; proximal aesthetasc much more slender

than in male; setal formula: 0.4.4.2.1.1.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 16P), second swimming leg, and exopod of fourth swimming leg (Fig. 16R) similar to male.

Third swimming leg (Fig. 16Q) with smooth praecoxa and intercoxal sclerite. Coxa with arched row of spinules on anterior surface but unarmed. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than entire exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, unornamented and unarmed, reaching only 1/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 16R) without spiniform process on basis. Endopod one-segmented, ornamented with apical row of several spinules at base of apical spine and few spinules on inner margin; apical spine not distinct at base, smooth, and about 0.8 times as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 16S) also simple cuticular plate, but with inner distal corner less sharp and without spinules along inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, completely fused, forming simple flap.

TYPE: Type material deposited in the National Institute of Biological Resources in Korea (collection numbers NIBRIV0000137623 and 0000137624), and Daegu University (collection numbers DB20026 and 20026).

TYPE LOCALITY: South Korea, Chungcheongbuk-do state, Danyang city, Ondal-gul cave.

DISTRIBUTION: Beside the type locality, Ondal-gul cave near Danyang city (central South Korea), Lee and Chang (2009) reported this species also from the interstitial of Namgang River near Haman (southern South Korea). In the light of the discovered short-range endemism in this group (Karanovic et al., 2012), the latter record is questionable. Miura's (1969) material, which was synonymised with *P. ondali* by Lee and Chang (2009), although not by Chang (2010), came from a well near Seongryugul cave at Uljin. This is very close to the type locality of *P. wangpi* (see below). The morphological similarities between Miura's drawings and this species lead Karanovic et al. (2012) to believe that the these populations are conspecific.

ECOLOGY: The specimens were obtained in a cave, but precise environment and environmental conditions are unknown.

REMARKS: Lee and Chang (2009) noted that *P. ondali* is probably most closely related to *P. nipponensis* from Japan, and listed seven major morphological differences. They did, however, admit that some of them may be a result of incomplete illustrations or observations of the latter species. Chang (2010) pointed out these four morphological differences between the two taxa: relative length of the caudal rami, number of setae on the female fifth leg, length of spine on the female third leg exopod, and relative length of the female fourth leg endopod. We think that second difference may also be a result of incomplete illustrations of *P. nipponensis*, but the two species differ sufficiently in the proportion of the caudal rami and the shape of the fifth leg to justify separate specific statuses. In the light of a newly discovered short-range endemism of this group in Korea, the Japanese population is most probably only a distant relative. For differences between *P. ondali* and three other Korean species see the remarks section for *P. young* below.

16. Proserpinicaris pannonica Török, 1935 (Fig. 17)

Parastenocaris pannonicus Török, 1935, p. 650, figs. 14, 15; Lang, 1948, p. 1239, fig. 496-6; Damian, 1958, p. 190, figs. 10, 11; Kulhavý, 1960, p. 301, fig. 9; Damian-Georgescu, 1970, p. 226, figs. 105, 106.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 480 to 510 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. No information available on somite ornamentation, rostrum, or anal operculum, although operculum probably convex as in female.

Caudal rami (Fig. 17A) about 2.2 times as long as greatest width (lateral view), mostly cylindrical but somewhat tapering towards distal end, unornamented, armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about 0.7 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/4 of ramus length. Proximalmost lateral seta placed more dorsally, 0.8 times as long as ramus, and twice as long as distal seta. Inner apical seta small, smooth, inserted more ventrally, about 0.9 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown. Outer apical seta also without breaking plane and smooth, relatively strong basally but much shorter, 1.8 times as long as caudal ramus.

Antennula, antenna, mandibula, maxillula, maxilla, and maxilliped unknown but probably similar to type species.

First swimming leg (Fig. 17B) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long spinule on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.6 times as long as entire endopod and only slightly longer than larger geniculate exopodal seta.

Second swimming leg (Fig. 17C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed and unornamented. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine (probably broken in Fig. 17C); second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one longest; all exopodal armature bipinnate. Endopod one-segmented, cylindrical, about five times as long as wide, reaching midlength of first exopodal segment, ornamented with one large spinule on outer margin and at least one large spinule on apical margin; armed apically with one smooth seta, about as long as segment.

Third swimming leg (Fig. 17D, E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, unarmed but ornamented with row of minute spinules along inner margin proximally. Endopod small, spiniform and smooth. Exopod with both segments fused; ancestral proximal segment twice

as long as wide, curved inwards, and with one large chitinous beak on inner margin proximally, ornamented with very large spinule at base on outer margin proximally; armed subapically with spiniform, slender, and smooth seta, slightly longer than apophysis and pointing outwards; ancestral distal segment (apophysis) cylindrical, also oriented inwards, unornamented and armed with single short smooth seta on top.

Fourth swimming leg (Fig. 17F) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with large chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long strong apical seta. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes distally, resembling some primitive, Stone-Age spear tips.

Fifth leg (Fig. 17G) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, 4.6 times as long as greatest width, ornamented with several large spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost 0.7 times as long as entire leg; middle seta (ancestral outer endopodal) 0.4 times as long as leg, and about 0.7 times as long as innermost seta (ancestral inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 530 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite. Other information on shape and ornamentation of somites missing.

Caudal rami, antennula, antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 17H), and exopod of fourth swimming leg (Fig. 17J) similar to male.

Third swimming leg (Fig. 17I) with large praecoxa, smooth coxa and intercoxal sclerite. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, small, linguiform, ornamented with several spinules apically but unarmed.

Fourth swimming leg (Fig. 17J) without spiniform process on basis. Endopod one-segmented, spiniform, smooth, not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg probably similar to that of male.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: Hungary, Budapest, probably interstitial around Danube River.

DISTRIBUTION: This species was described originally from Budapest (Hungary), but was later found near Bucharest (Romania) and in a small river in eastern Slovakia (Török, 1935; Damian, 1958; Kulhavý, 1958). It seems that its distributional range is in the lower parts of the Danube River drainage area.

ECOLOGY: The type material was collected from the water pipes in Budapest, Hungary (Török, 1935), which means that the species' habitat is probably interstitial around the Danube River. Material from Romania also came from the water supply of the capital city (Damian, 1958), while samples from



Fig. 17. *Proserpinicaris pannonica*. Male: A. caudal ramus, lateral view; B. first swimming leg; C. second swimming leg; D. exopod of third swimming leg; E. third swimming legs; F. basis, endopod and first exopodal segment of fourth swimming leg; G. fifth leg. Female: H. second swimming leg; I. third swimming leg; J. fourth swimming leg. Scales: unknown (cited from Damian, 1958, modified).

eastern Slovakia were collected from a small stream. Thus, it seems this species is tolerant of a wide range of environmental factors in its interstitial environment, which it must be to survive in the lower parts of one of the most polluted European rivers. The Slovakian record in a small stream gives hope that this species may survive even though some populations along the Danube may have become extinct as a result of increased pollution in the second half of the 20th century.

REMARKS: Lang (1948) considered this species a member of the *minuta* group, but that was probably because of an incorrect interpretation of the fourth leg armature and ornamentation in male by Török (1935), who illustrated the basal chitinous process as being inwards from the endopod. Damian (1958) redescribed this species and correctly grouped it together with *P. proserpina*, *P. nolli*, *P. phyllura*, etc., although she did not discuss major morphological differences between these species. We believe that the shape of the third leg in male and, to a certain degree, the armature and ornamentation of the fifth leg are different enough from any species of the genus *Proserpinicaris* to justify its separate specific status. The species, of course, is in urgent need of redescription based on newly collected material.

17. Proserpinicaris phyllura Kiefer, 1938 (Fig. 18)

Parastenocaris phyllura Kiefer, 1938, p. 147, figs. 15–23; Kunz, 1938, p. 151, figs. 2–15; Lang, 1948, p. 1246, fig. 500-3; Noodt, 1952, 338, figs. 29–36; Kulhavý, 1960, p. 299, fig. 6; Dussart, 1967, p. 421, fig. 187; Enckell, 1969, p. 499; Glatzel, 1990, p. 134, fig. 1; Glatzel, 1992, p. 185, figs. 1–5; Glatzel and Schminke, 1996, p. 104, figs. 1–5.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 580 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 18A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about 9.5; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), presence of cuticular window unknown. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax about 1.8 times as long as wide in dorsal view; representing 18% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally not known.

Urosomal somites (except preanal, which unornamented) with at least pair of lateral posterior sensilla and with smooth hyaline fringes, but exact number and position of sensilla and pores unknown.

Anal somite (Fig. 18B, C) ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened smooth.

Caudal rami (Fig. 18B, C) laterally compressed and inflated in lateral view, foliaceous, about three times as long as greatest width (dorsal view) and almost 1.8 times as long as anal somite, parallel, with space between them about one ramus width, unornamented; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6, about 0.4 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/4 of ramus length. Proximal lateral seta placed more dorsally, 0.3 times as long as ramus, and 2.3 times as long as distal one. Inner apical seta smooth, inserted more ventrally, about as long as dorsal seta. Middle apical seta strongest, without breaking plane, smooth, 1.7 times as long as ramus. Outer apical seta also without breaking plane but much more slender, relatively strong basally, 0.6 times as long as ramus. Caudal rami shape can be variable (Fig. 18D), as can length and exact position of lateral setae.

Antennula relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process, but small spiniform process present on fourth segment proximally. Armature unknown.

Antenna, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown but probably similar to type species.

Second swimming leg (Fig. 18E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin and another one on inner margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae). Endopod one-segmented, cylindrical and long, almost nine times as long as wide, reaching 2/3 of first exopodal segment in length, ornamented with few large spinules along apical margin and one on outer margin; armed apically with one smooth seta, about as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 18F, G) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, partly fused to coxa, armed with outer seta and ornamented with row of large spinules on outer margin distally; additional row of small spinules along inner margin proximally. Endopod a minute but distinct segment, spiniform, slightly curved, about as long as largest spinule on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and with large chitinous beaks on inner margin at midlength, ornamented with several large spinules along outer margin, armed subapically with simple, strong, smooth, sharp and straight spine, slightly longer than apophysis; ancestral distal segment (apophysis) cylindrical, oriented inwards, unornamented and armed with single short seta on top, distal tip like small ball.

Fourth swimming leg (Fig. 18H, I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with huge, inwards-pointing chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membrane and distally, resembling some primitive, Stone-Age knife; considerably longer than spiniform process on basis and pointing distally.



Fig. 18. *Proserpinicaris phyllura*. Male: A. habitus, dorsal view; B. last three urosomal somites and caudal rami, dorsal view; C. last three caudal somites and caudal rami, lateral view; D. caudal rami, lateral view; different specimen; E. second swimming leg without last two exopodal segments; F. third swimming leg; G. distal part of third swimming leg; H. fourth swimming leg without last two exopodal segments; I. fourth swimming leg without last two exopodal segments, different specimen; J. male and female in copula. Female: K. anal somite and caudal rami, dorsal view; L. anal somite and caudal rami, lateral view; M. fifth leg. Scales: unknown (cited from Kiefer, 1938, Kunz, 1938, and Glatzel and Schminke, 1996, modified).

Fifth leg (Fig. 18M) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, ornamented with spinules along inner margin, armed with three smooth setae; outermost seta (ancestral basal one) longest, as long as entire leg; middle seta (ancestral outer endopodal) 0.4 times as long as leg, and 1.9 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, probably also around 580 μ m. Habitus (Fig. 18J), ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender. Anal somite (Fig. 18K, L) more elongated.

Caudal rami (Fig. 18K, L) relatively similar to male, but generally more laterally compressed and divergent, less inflated in lateral view, and shorter in proportion to anal somite; about 3.5 times as long as wide.

Antennula also seven-segmented, ornamentation and armature unknown.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg similar to male.

Third swimming leg with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with few spinules apically, unarmed.

Fourth swimming leg without spiniform process on basis. Endopod one-segmented, ornamented with apical row of several spinules at base of apical spine, distinct at base, bipinnate, and about as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg also simple cuticular plate, but with inner distal corner more produced posteriorly and without spinules along inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material exists in the Kiefer Collection, Staatliches Museum für Naturkunde, Karlsruhe, Germany (Franke, 1989).

TYPE LOCALITY: Germany, northwestern Bavaria, Aschaffenburg, well in Schönbusch Park.

DISTRIBUTION: Enckell (1969) studied the distribution of parastenocaridids in central and northern Europe in fine detail and reported this species from Germany, Czech Republic, Slovakia, Netherlands, Denmark, Sweden, Norway and Finland. Apparently this species is widely distributed in central and northern Europe, and the lack of data from Poland or Estonia, for example, is only a consequence of the lack of appropriate surveys in these and other neighbouring countries.

ECOLOGY: *Proserpinicaris phyllura* is one of the few parastenocaridid species that can be found in slightly brackish habitats, in addition to fresh groundwater (Enckell, 1969; Glatzel, 1990), although it is not clear whether the species actually lives in the brackish water or in the top layer of fresh water that usually floats on top in these anchialine environments. According to Enckell (1969), the species does not occur above the highest shore line in Fennoscandinavia.

REMARKS: Kiefer (1938) did not discuss affinities of his new species, but Kunz (1938) noted its

close relationship with *P. proserpina* and *P. cantabrica*, for which he proposed the *proserpina* group. This group was accepted by Lang (1948), who added two more species to it, and proposed seven other groups. *Propserpinicaris phyllura* can be distinguished from all other members of the group by its laterally compressed caudal rami, and to a lesser degree details in shape and ornamentation of the male third and fourth legs. This is certainly one of the best-studied species of parastenocaridids so far. Enckell (1969) mapped its distribution in fine detail and collected much useful data on its habitat preferences. Glatzel (1990) studied its locomotion, grooming behavior, moulting, and reproduction. Glatzel (1992) described the nauplius stages, while Glatzel and Schminke (1996) reported on its mating behavior.

18. *Proserpinicaris proserpina* Chappuis, 1938 (Figs. 19, 20)

Parastenocaris proserpina Chappuis, 1938, p. 177, figs. 54–64; Lang, 1948, p. 1244, fig. 500-1; (?) Kulhavý, 1960, p. 300, fig. 7; Dussart, 1967, p. 435, fig. 198; Bruno and Cottarelli, 1998, p. 126, figs. 4–6, 10A–D, F.

Proserpinicaris proserpina (Chappuis): Jakobi, 1972, p. 134; Schminke, 2010, p. 352.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 380 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about 8.8; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax about 1.6 times as long as wide in dorsal view; representing 20% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally not known.

Urosomal somites (except preanal, unornamented) with eight posterior sensilla and with smooth hyaline fringes.

Anal somite (Fig. 19A) ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with almost straight and smooth distal margin, not reaching posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened smooth.

Caudal rami (Fig. 19A, B) about 2.3 times as long as greatest width (dorsal view) and almost 0.7 times as long as anal somite, mostly cylindrical but slightly inflated at midlength, divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three

lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other but at 1/4 of ramus length. Proximalmost lateral seta placed more dorsally, 1.2 times as long as ramus, about seven times and long as middle seta (minute), and 1.3 times as long as distalmost (ventralmost) one. Inner apical seta smooth, inserted more ventrally, about 0.9 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, exact length unknown but much longer than ramus. Outer apical seta also without breaking plane but unipinnate, relatively strong basally, 1.6 times as long as ramus. Caudal rami shape variable, and sometimes very inflated, with most setae reduced in size.

Antennula (Fig. 19C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process, but small spiniform process present on fourth segment proximally. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.7.4.2.0.0.6. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 19D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed but ornamented with two large spinules proximally on anterior surface. Endopod half as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula (Fig. 19E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 19F) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 19G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong and pinnate claw, probably without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 19H) with very strong and relatively long syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 19I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on inner margin, and armed with single short seta on outer margin. Exopod three-segmented,

armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 19J) with smooth praecoxa, and intercoxal sclerite. Coxa with posterior row of minute spinules. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.2 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, almost seven times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with few large spinules along apical margin and one on outer margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 20A) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with outer seta and ornamented with diagonal row of large spinules close to outer margin; additional few small spinules on anterior surface and row of small spinules along inner margin proximally. Endopod minute but distinct segment, curved, about twice as long as largest spinule on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and, with two large chitinous beaks on inner margin distally, unornamented, armed subapically with simple, strong, smooth and inwards-curved spine, significantly longer than apophysis; ancestral distal segment (apophysis) conical, oriented slightly inwards, unornamented and armed with single short seta on top.

Fourth swimming leg (Fig. 20B, C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.9 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, but very elaborately decorated with serrulate membranes proximally and distally, resembling some primitive, Stone-Age spear tips; considerably shorter than spiniform process on basis.

Fifth leg (Fig. 20D) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, ornamented with several spinules along inner margin and cuticular pore on anterior surface, armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.1 times as long as entire leg; middle seta (ancestral outer endopodal) 0.4 times as long as leg, and 1.3 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 380 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double



Fig. 19. *Proserpinicaris proserpina*, Male. A. anal somite and caudal rami, dorsal view; B. right caudal ramus, lateral view; C. antennula; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg. Scales: 25 μ m (cited from Bruno and Cottarelli, 1998, modified).



Fig. 20. *Proserpinicaris proserpina*. Male: A. third swimming leg; B. fourth swimming leg; C. fourth swimming leg without last two exopodal segments, different specimen; D. fifth leg. Female: E. right caudal ramus, lateral view; F. antennula; G. second swimming leg without last two exopodal segments; H. third swimming leg; I. fourth swimming leg; J. fifth leg. Scales: A, B, D–J=25 μ m, C=unknown (cited from Chappuis, 1938, and Bruno and Cottarelli 1998, modified).

somite and habitus slightly less slender.

Genital double somite slightly longer than wide (dorsal view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami (Fig. 20E) very similar to male, but generally more inflated in lateral view.

Antennula (Fig. 20F) also seven-segmented, unornamented, with slender aesthetasc on fourth segment, not reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula: 0.4.4.2.0.0.6. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg (Fig. 20G), and exopod of fourth swimming leg (Fig. 20I) similar to male.

Third swimming leg (Fig. 20H) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, ornamented with few spinules apically, unarmed, reaching only 1/5 of first exopodal segment in length.

Fourth swimming leg (Fig. 20I) without spiniform process on basis. Endopod one-segmented, ornamented with apical row of several spinules at base of apical spine, distinct at base, bipinnate, and about 0.8 times as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 20J) also simple cuticular plate, but with inner distal corner more produced posteriorly and without spinules along inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material probably lost.

TYPE LOCALITY: Italy, Salerno, Pertosa, Grotta dell'Angelo cave.

DISTRIBUTION: Bruno and Cottarelli (1998) reported and redescribed this species from numerous localities in central and southern mainland Italy (Tuscany, Lazio, Campania, Apulia and Basilicata regions), although they were not successful in obtaining material from the type locality (Grotta dell'Angelo cave, Pertosa near Salerno). Interestingly, the senior author of this monograph also visited this cave in 1999, but did not find any specimens of *P. proserpina*. The record of this species in Slovakia by Kulhavý (1960) is questionable (see the synonymy section above), as he only found females. If he indeed found a member of the genus *Proserpinicaris*, it would most likely be a separate endemic species.

ECOLOGY: Specimens were obtained from wells, hyporheic, and groundwater habitats, as well as from lake beaches, using various methods. This tells us about its wide ecological tolerance for many environmental factors, such as dissolved oxygen, temperature, water movement, and even water chemistry. Bruno and Cottarelli (1998) documented a wide variability in the caudal rami shape and

also, to a lesser extent, in the shape and armature of the third and fourth legs in male, which may be indicative of multiple species in this complex, especially given its presumed wide distributional range. This species would be a very good candidate to test interpopulation and regional variability hypotheses with molecular tools.

REMARKS: Bruno and Cottarelli (1998) noted that *P. proserpina* is probably most similar morphologically to *P. amalasuntae*, with which it can even be found sympatrically in some localities in Italy. The main differences include the fine details in shape and ornamentation of the male third and fourth legs, which are sexually dimorphic characters. The endopod of the fourth legs seems to be the main distinguishing feature between these two closely related taxa, as it is much longer and more robust in *P. amalasuntae* (i.e., as long as or slightly longer than the first exopodal segment).

19. Proserpinicaris wangpi Karanovic, Cho and Lee, 2012 (Figs. 21–23)

Parastenocaris nipponensis Chappuis: Miura, 1969, p. 253, figs. 47–51. *Proserpinicaris wangpi* sp. nov., Karanovic et al. (2012).

Male: Total body length from 355 to 373 μ m. Colour, body segmentation, arthrodial membranes, and sensilla pattern as in *P. young* (see below). Habitus (Fig. 21A) cylindrical and slender, without any demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width hard to establish in dorsal view; free prosomites in lateral view narrower than cephalothorax or even slightly than urosome. Body length/width ratio about 8.8; cephalothorax about as wide as genital somite. Free pedigerous somites without any expansions laterally or dorsally. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes, except in preanal somite dorsally and partly laterally. Integument weakly sclerotized, very smooth, without any spinules or cuticular pits (except few spinules on caudal rami), ornamentated with 45 pairs of sensilla and four pairs pores (three on anal somite, and one on caudal rami), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites, all in same position and of similar size as in *P. young*. Pleural areas of cephalothorax (Fig. 21D) and free pedigerous somites (Fig. 21A) not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view; rostrum and cuticular sutures of free pedigerous posomites as in *P. young*.

Cephalothorax (Fig. 21A, D) about 1.5 times as long as wide in dorsal view; representing 17% of total body length.

Urosomites (Figs. 21A, 22A, B, 23A) proportionately shorter and wider than in *P. young*, but without any other difference. Anal somite also about 1.2 times as long as preanal somite.

Spermatophore (Fig. 23A) proportionately smaller and more slender than in P. young.

Caudal rami (Figs. 21B, 23A) much shorter than in *P. young* (arrowed in Fig. 23A), about 4.3 times as long as greatest width (ventral view) and about 1.2 times as long as anal somite, cylindrical, parallel, with space between them about 1.5 times one ramus' width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large lateral cuticular pore near posterior margin, and posterior ventral row of three large spinules. Dorsal seta slender and smooth, inserted closer to inner margin of ramus at about 5/6 of its length, 1.3 times as long as caudal ramus, triarticulate basally. Lateral setae slender and smooth, inserted very close to each other at 2/5 of ramus length, two larger ones more anteriorly and minute one in between and slightly more



Fig. 21. *Proserpinicaris wangpi*, Holotype male. A. habitus, ventral view; B. anal somite and caudal rami, ventral view; C. antennula, ventromedial view; D. mouth appendages, ventral view; E. distal tips of third swimming legs and exopod of left fourth leg, ventral view; F. coxa, intercoxal sclerite, basis, and endopod of fourth swimming leg, anterior view. Scales: A=30 μ m, B, C=10 μ m, D=3 μ m, E, F=2 μ m (All SEM micrographs original).



Fig. 22. *Proserpinicaris wangpi*. Holotype male: A. fifth pedigerous and genital somites, ventral view. Paratype male: B. fifth legs, lateral view. Allotype female: C. habitus, lateral view; D. anal somite and caudal rami, lateral view. Scales: A, D=10 μ m, B=3 μ m, C=20 μ m (All SEM micrographs original).

posteriorly. Anterior lateral seta which inserted more dorsally longest, 0.7 times as long as ramus, 1.4 times as long as other anterior seta, and about seven times as long as minute (distal) seta. Inner apical seta smooth, inserted close to ventral margin, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, unipinnate, about 1.5 times as long as ramus, pointing distally, with slightly curled tip. Outer apical seta also without breaking plane and unipinnate, relatively strong basally but much shorter, about 0.7 times as long as ramus, inserted close to dorsal surface and pointing laterally.

Antennula (Fig. 21C) relatively large, eight-segmented, prehensile and digeniculate, with distal part much more strongly clasped and fifth segment more robust than in *P. young*, but armature and ornamentation without any difference, except aesthetasc on fifth segment wider and slightly longer.

Antenna, labrum (Fig. 21D), mandibula (Fig. 21D), maxillula (Fig. 21D), maxilla (Fig. 21D), maxilliped (Fig. 21D), and first swimming leg as in *P. young*.



Fig. 23. *Proserpinicaris wangpi*. Paratype male: A. urosome, lateral view; B. third swimming leg, posterior view; C. endopod of second swimming leg, anterior view. Paratype female: D. ventral part of genital double-somite, lateral view; E. right caudal ramus, lateral view; F. last four antennal segments with incomplete armature, ventral view; G. endopod of second swimming leg, anterior view; H. third swimming leg, anterior view; I. endopod of third swimming leg, anterior view; J. endopod of fourth swimming leg, anterior view. Arrows pointing features different from other Korean short range endemics. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 50 μ m.

Paragnaths (Fig. 21D) with eight large spinules in transverse row on posterior surface of central lobe.

Second swimming leg (Fig. 23C) as in *P. young*, except endopod only about four times as long as wide (arrowed in Fig. 23C) and reaching 3/5 of first exopodal segment; apical seta 0.7 times as long as segment and pointing distally.

Third swimming leg (Figs. 21E, 23B) with narrower basis and proximal exopodal segment (arrowed in Fig. 23B) than in *P. young*, and with shorter outer spine on proximal exopodal segment. Proximal exopodal segment 2.7 times as long as wide, with small tubular pore on posterior surface near inner margin (latter not observed in *P. young*). Distal outer corner of proximal exopodal segment smooth (spinule missing). Leaf-like seta on apophysis more curved than in *P. young*.

Fourth swimming leg (Fig. 21F) as in *P. young*, except apical seta on third exopodal segment somewhat shorter (about 2.2 times as long as third exopodal segment and 0.6 times as long as entire exopod); endopod and large basal spiniform process exactly as those in *P. young*.

Fifth leg (Fig. 22A, B) simple triangular cuticular plate, inner distal corner produced into distally serrate spiniform process (which shorter than in *P. young*), ornamented with four large spinules on inner margin, one arched proximal row of 14 minute spinules on posterior surface, and large cuticular pore on anterior surface; armature as in *P. young*.

Sixth legs (Fig. 22A) smooth, unarmed and unornamented, forming simple operculum covering gonopore, slightly smaller than in *P. young*.

Female: Body length from 330 to 355 μ m. Habitus (Fig. 22C), ornamentation of prosomites, colour, and nauplius eye similar to male; genital and first abdominal somite fused into double somite and habitus less slender; free prosomites significantly narrower than urosomites in lateral view.

Genital double somite (Figs. 22C, 23D) about as wide as long (dorsal view), without any trace of subdivision, with oval dorsal cuticular window in anterior half, which much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures covered by vestigial sixth legs; median copulatory pores also covered by fused sixth legs; seminal receptacles small, trapezoidal in lateral view, hard to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotized. All posterior senislla homologous to those on male third urosomite, while two sensilla from male second urosomite missing (Nos. 32 and 34).

Third (Fig. 22C), fourth (preanal) (Fig. 22C), and fifth (anal) (Fig. 22D) urosomites similar to male.

Caudal rami (Figs. 22D, 23E) slightly shorter in proportion to anal somite, from 3.6 to 3.9 times as long as wide, but also cylindrical and parallel, with armature and ornamentation as in male.

Antennula (Figs. 22C, 23F) segmentation, ornamentation, and armature as in *P. young*, except both easthetascs much more robust (arrowed in Fig. 23F).

Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, exopod of fourth swimming leg similar to male.

Third swimming leg (Figs. 22C, 23H) as in *P. young*, but with shorter apical element on second exopodal segment (arrowed in Fig. 23H).

Fourth swimming leg (Figs. 22C, 23) without spiniform process on basis. Endopod one-segmented, slightly curved, ornamented with apical row of two spinules at base of apical spine and three spinules on inner margin; apical spine not distinct at base, finely serrated (or bipinnate) distally, and about as long as endopod (i.e. proportionately longer than in *P. young*; arrowed in Fig. 23J).

Fifth (Fig. 22C) and sixth legs as in P. young.

TYPE LOCALITY: South Korea, Gyungsangbuk-do region, Uljin city, Geunnam town, Wangpi stream, interstitial from several beaches on banks, 36° 57′41.4″N 129° 22′46.4″E.

DISTRIBUTION: Beside the type locality, Wangpi stream near Uljin city (South Korea), this species probably lives also in a well near Seongryu-gul cave at Uljin (less than 15 km away). Miura (1969) reported the latter population as *P. nipponensis* Chappuis, 1955, and Lee and Chang (2009) synonymised it with their new species *P. ondali* Lee and Chang, 2009. In the light of the newly discovered short-range endemism in this group, both were probably wrong. Most morphological characters agree with *P. wangpi*, and the proximity of these two locations suggests that they are conspecific. Thus, we think Miura's record is likely to be synonymous with this species.

ECOLOGY: Specimens were obtained from several interstitial samples as well as from a well near a cave, which probably means that this species exploits a wide range of subterranean environments.

SPECIMEN EXAMINED: Types only: holotype male, allotype female, three paratypes (one male and three females) together on 1 SEM stub (collection number NIBRIV0000232619); four paratypes (one males and three females) dissected on one slide each (collection numbers NIBRIV0000232620 to 0000232623); additional three paratype females together in alcohol (NIBRIV0000232624); 12 paratypes from separate sample (two males, six females and four copepodids) together in alcohol (NIBRIV00 00232625); all collected from type locality, 18 May 2010, leg. J.-L. Cho, all deposited in the National Institute of Biological Resources, South Korea.

REMARKS: *Proserpinicaris wangpi* is apparently very closely related to the Korean *P. ondali* Lee and Chang, 2009, as well as to two other short-range endemics described by Karanovic et al. (2012), *P. imjin* and *P. young* (see above and below). Their morphological differences are discussed in the remarks section for *P. young* (see below).

20. Proserpinicaris young Karanovic, Cho and Lee, 2012 (Figs. 24–29)

Proserpinicaris young sp. nov., Karanovic et al. (2010).

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 375 to 406 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites (first pedigerous fused to cephalothorax)), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Podoplean boundary between prosome and urosome inconspicuous. Habitus (Figs. 24A, 26A) cylindrical and very slender, without any demarcation between prosome and urosome; prosome/urosome ratio about 0.9 in dorsal view; greatest width in dorsal view at fourth and fifth pedigerous somites, but hard to establish; free prosomal somites in lateral view narrower than cephalothorax or urosome. Body length/width ratio about 8.1; cephalothorax about as wide as genital somite. Free pedigerous somites without any lateral or dorsal expansions, all connected by well developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes, especially dorsally, except in preanal somite, where hyaline fringe well developed dorsally and partly laterally, but not ventrally (Figs. 24A, 26A, 27A, B). Integument weakly sclerotized, smooth, ornamented only with sensilla and pores (no spinules or cuticular pits), with round dorsal double cuticular window on cephalothorax, and oval dorsal simple cuticular windows on genital and three postgenital somites. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and

coxae of swimming legs clearly exposed in lateral view.

Rostrum (Fig. 26C) small, membranous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax (Figs. 24A, E, 26A–C) about 1.8 times as long as wide in dorsal view; representing 21% of total body length. Surface of cephalic shield ornamented with 16 pairs of large sensilla (numbered from anterior to posterior and from dorsal to ventral side in Fig. 26B, C); no small sensilla, cuticular pores, pits, or any other ornamentation; five pairs of sensilla surround double cuticular window, but its surface completely smooth; all except one pair of sensilla (No. 11) visible from dorsal view. Athroidal membrane between cephalothorax and second pedigeous somite (first free) larger than between any other somites.

Second pedigerous somite (Figs. 24A, 26A–C) as wide as posterior half of cephalothorax in dorsal view, with four pairs of large sensilla (three dorsal and one lateral; Nos. 17–20), and with arched dorsal sutures in anterior half joining to make interesting crown-like pattern.

Third pedigerous somite (Figs. 24A, 26A–C) slightly wider and longer than second pedigerous, with five pairs of large sensilla (Nos. 21–25), also with arched dorsal sutures making crown-like pattern, but less pronounced than in second pedigerous somite.

Foruth pedigerous somite (Figs. 24A, 26A–C) widest prosomal somite in dorsal view, slightly longer than third prosomal, with only three pairs of large posterior sensilla (Nos. 26–28), with deeper and longer arched sutures than in any other segment.

First urosomite (Figs. 24A, D, 27A, B) about as wide as fourth pedigerous but slightly shorter, also with three pairs of large posterior sensilla (Nos. 29–31), with two small arched dorsal sutures in anterior half, and with nearly continuous horizontal suture in posterior half at level of sensilla insertion.

Second urosomite (= genital somite) (Figs. 24A, D, 27A, B) slightly narrower and shorter than first urosomite, with oval dorsal cuticular window in anterior half, also with three pairs of posterior sensilla (Nos. 32–34), but two dorsal pairs (Nos. 32 and 33) closer to each other than in first urosomite.

Third urosomite (Figs. 24A, 27A, B) about as long as second urosomite but slightly narrower, with shorter and wider dorsal cuticular window, and with five pairs of large posterior sensilla (Nos. 35–39); two dorsal pairs (Nos. 32 and 33) much closer to each other than in second urosomite.

Foruth urosomite (Figs. 24A, 27A, B) slightly narrower than third urosomite, but also with five pairs of large posterior sensilla (Nos. 40–44), and with similar size dorsal cuticular window.

Fifth urosomite (= preanal somite) (Figs. 24A, 27A, B) slightly narrower and longer than fourth urosomite, with largest dorsal cuticular window of all urosomite, and without any surface ornamentation.

Sixth urosomite (= anal somite) (Figs. 24A, 25A, 27A, B) about 1.2 times as long as and slightly narrower than preanal somite, ornamented with pair of large dorsal sensilla at base of anal operculum, pair of large lateral cuticular pores in anterior half, pair of ventral pores at base of caudal rami, and pair of minute ventro-lateral pores in posterior eighth of somite length (no spinules on ventral surface). Anal operculum well developed, unornamented on outer surface, with smooth and almost straight distal margin, not reaching posterior end of anal somite, representing 70% of somite's width. Anal sinus wide opened, ornamented with two long diagonal rows of slender spinules on ventral side, and two parallel rows on dorsal side (inner side of anal opeculum).

Spermatophore (Fig. 26D) about twice as long as wide, kidney-shaped, with narrow and curved neck. Note, spermatophore neck and its opening squeezed out and visible in upper right corner in Fig. 1D.



Fig. 24. *Proserpinicaris young*. Holotype male: A. habitus, lateral view; B. distal tips of third swimming legs; C. fourth swimming legs, ventrolateral view; D. fifth and sixth legs, ventrolateral view. Paratype male 1: E. antennulae, anterior view. Paratype male 2: F. detail of left antennula, lateral view. Scales: A=30 μ m, B, F=1 μ m, C=2 μ m, D, E=10 μ m (All SEM micrographs original).

Caudal rami (Figs. 24A, 25A, 27A, B) very long and slender, about six times as long as greatest width (ventral view) and about 1.4 times as long as anal somite, cylindrical, parallel or slightly divergent, with space between them about twice that of one ramus width; armed with seven elements (three lateral, one dorsal, and three apical). Ornamentation consists of large lateral cuticular pore near posterior margin, and posterior ventral row of several spinules along posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4, about 0.8 times as long as caudal ramus, triarticulate basally. Lateral setae slender and smooth, inserted very close to each other at 2/5 of ramus length, two larger ones more anteriorly and minute one in between and more posteriorly. Anterior lateral seta which inserted more dorsally longest, half as long as ramus, 1.4 times as long as ventral anterior seta, and about nine times as long as minute (distal) seta. Inner apical seta strongest, without breaking plane, unipinnate, about 1.7 times as long as ramus, pointing distally, with slightly curled tip. Outer apical seta also without breaking plane and unipinnate, relatively strong basally but much shorter, about 0.8 times as long as ramus, inserted close to dorsal surface and pointing laterally.

Antennula (Figs. 24E, F, 28A) slightly longer than cephalothorax, slender, eight-segmented, prehensile and strongly digeniculate, ornamented with four ventral spinules on first segment distally, and with ribbed elongated chitinous plate on anterior surface of sixth segment. First segment very short, while second longest. Geniculation between third and fourth and between sixth and seventh segments; last two segments in line. Distal anterior corner of seventh segment produced into very small spiniform process, but larger proximal spiniform process present on fifth segment on anterior surface. Massive aesthetasc on fifth segment reaching beyond tip of appendage, fused basally to slightly shorter seta, with nipple distally; much shorter and more slender apical aesthetasc on seventh segment, fused basally to two setae (acrotheck). Setal formula: 0.6.4.2.6.1.1.9. All setae slender and all, except largest seta on second segment and proximalmost seta on fifth segment, smooth; most setae with pore on tip; proximallmost seta on second segment longest and strongest, unipinnate with extremely long spinules along anterior surface.

Antenna (Figs. 24E, 28B) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about three times as long as wide, unarmed but ornamented with two rows of large spinules on anterior surface, and one short row of minute spinules on posterior surface. Endopod half as long as allobasis and twice as long as wide, with surface frill subdistally, ornamented with large spinules along anterior surface, armed laterally with two short spines (proximal one shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, which twice as long as segment. All antennal armature unipinnate.

Labrum (Fig. 24A) large and triangular in lateral view, with narrow and straight cutting edge, without any ornamentation on anterior surface, with several parallel rows of spinules along cutting edge (those on outer distal corners strongest).

Paragnaths (Fig. 24A) strongly fused into trilobite structure, with numerous distal rows of slender short spinules on lateral lobes, one distal row of minute spinules on central lobe, and another transverse row of 10 very long spinules on posterior surface of central lobe at about 2/3 of its length.

Mandibula (Figs. 24A, 28C, D) with narrow cutting edge on elongated coxa, armed with one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules in between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on tip.

Maxillula (Figs. 24A, 28E) with relatively large praecoxa, arthrite rectangular, about 1.5 times as

long as wide from lateral view, ornamented with single spinule on posterior surface near dorsal margin, armed with lateral strong seta and four apical elements (probably three spines and one strong seta; apical spines with crown of spinules on tip, resembling small hands). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical setae (two smooth and slender, one curved and unipinnate), and single minute lateral seta. Endopod and exopod absent (fused to basis without trace), minute seta on basis probably representing remnants of exopodal armature. All coxal and basal setae, as well as smooth lateral seta on praecoxa, with pore on tip.

Maxilla (Figs. 24A, 28F), composed of syncoxa, basis, and one-segmented endopod, ornamented with row of five spinules on inner side of syncoxa proximally, and with arched row of six spinules on posterior side of suncoxa close to outer margin. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with two smooth and one pinnate seta apically. Basis drawn out into strong and unipinnate claw, without seta at base, with cuticular pore on convex margin near distal tip. Endopod represented by minute segment, armed with two smooth subequal apical setae. All setae on maxilla with pore on tip.

Maxilliped (Figs. 24A, 28G) with short and relatively strong syncoxa, unarmed and unornamented; basis slender, almost five times as long as wide and three times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, ornamented with several strong spinules along concave margin distally, about 0.7 times as long as basis.

First swimming leg (Figs. 24A, 29A) with smooth praecoxa, coxa, and intercoxal sclerite. Intercoxal sclerite very small, with narrow and concave distal margin. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch along distal margin at base of endopod, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin and distally on all segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one longer row of even longer spinules on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod, 1.2 times as long as larger geniculate exopodal seta, and almost 2.4 times as long as outer spine on endopod. All exopodal and endopodal armature unipinate along outer margin.

Second swimming leg (Figs. 24A, 29B) with smooth praecoxa, and intercoxal sclerite. Intercoxal sclerite large, trapezoidal, with deeply concave distal margin. Praecoxa triangular and large. Coxa short, rhomboidal, with diagonal row of small spinules on anterior surface and two shorter rows of minute spinules along distal margin on posterior surface. Basis larger than coxa, semicircular, unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with distal hyaline frills on each segment on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one slightly longer than exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, almost five times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with four large spinules along apical margin; armed apically with single smooth seta, which about 0.6 times as long as segment and pointing inwards.

Third swimming leg (Figs. 24B, 29C) with smooth intercoxal sclerite, which largest of all legs, trape-

zoidal, smooth, and with almost straight distal margin. Praecoxa not well defined on anterior surface, triangular on posterior surface, about as large as in second leg, unarmed, ornamented with single spinule on anterior surface. Coxa rectangular, with arched row of large spinules on anterior surface. Basis robust, ornamented with two minute spinules and one pore on anterior surface, several minute spinules along distal margin on posterior surface, armed with outer long and slender seta; distal inner corner of basis produced distally as short blunt chitinous beak, probably reinforcing exopod. Endopod represented with single smooth and strong armature element, inserted on inner margin at 1/3 of basis length. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and with inner chitinous bulge on at 2/3 of its length, ornamented with several minute spinules along outer margin, and single small spinule on distal outer corner, armed subapically with simple, strong, smooth and inwardly curved spine, which 1.6 rimes as long as apophysis; ancestral distal segment (apophysis) conical, oriented slightly inwards, unornamented, and armed with single short seta on top, which leaf-like, with its tip pointing outwards.

Fourth swimming leg (Figs. 24C, 29D) with smooth praecoxa and intercoxal sclerite. Intercoxal sclerite shorter and smaller than in second leg, with equally long and concave distal margin. Praxoca, large and triangular from anterior view. Coxa rhomboidal, slightly smaller than in second leg, unarmed, ornamented with short distal row of spinules on posterior surface. Basis also short and rhomboidal in anterior view, armed with single outer seta, ornamented with several spinules on outer margin and with huge chitinous spiniform process between exopod and endopod, which pointing inwards and leaf-like distally. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side of second and third segments; first segment with straight inner margin, additionally ornamented with long row of long and slender spinules along inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and long and strong apical seta 2.7 times as long as third exopodal segment, 0.8 times as long as entire exopod, and more than twice as long as outer spine. Endopod shorter than spiniform process on basis, one-segmented and spiniform, with apical crown of four large spinules, which fused basally and arranged as small scoop, pointing outwards. Apical endopodal scoop and tip of basal hyaline spine forming pincer-like structure.

Fifth leg (Figs. 24D, 27B) simple elongated triangular plate, inner distal corner produced into very long and and distally serrate spiniform precess, ornamented with short row of six large spinules along inner margin, longer row of smaller spinules on posterior surface proximally, and cuticular pore on anterior surface, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; middle seta (probably ancestral outer endopodal) much shorter than basal seta, hardly reachin tip of inner distal process, 0.2 times as long as leg, and 1.7 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, pointing caudally, and almost reaching distal margin of sixth legs with their tips.

Sixth legs (Fig. 24D) smooth, unarmed and unornamented, forming simple operculum covering gonopore, probably both fused together, or right one reduced and left one enlarged.

Female: Body length, excluding caudal setae, from 375 to 400 μ m. Habitus (Fig. 25B), ornamentation of prosomites, colour and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite (Figs. 25B, E, 27C) about as wide as long (dorsal view), without any trace of subdivision, with oval dorsal cuticular window in anterior half, which much larger than that in male (originating from fused windows of two ancestral somites). Genital complex (Fig. 25E) occupying anterior ventral half of genital double somite; genital apertures covered by vestigial sixth legs; median copulatory pores also covered by fused sixth legs; seminal receptacles small, hard to distin-


Fig. 25. *Proserpinicaris young*. Paratype male 2: A. anal somite and caudal rami, lateral view. Paratype female 1: B. habitus, dorsal view. Paratype female 2: C. anal somite and caudal rami, posterior view. Allotype female: D. anal somite and caudal rami, ventral view; E. fifth legs and genital area, ventral view; F. mouth appendages, ventral view. Scales: A, C-F=10 μ m, B=100 μ m (All SEM micrographs original).



Fig. 26. *Proserpinicaris young*. Paratype male 3. A. habitus, dorsal view; B. prosome with most appendages omitted, lateral view; C. prosome, dorsal view; D. spermatophore. Arabic numerals numbering sensilla consecutively from anterior to posterior end of body, and from dorsal to ventral side. Scales: 100 μ m.



Fig. 27. *Proserpinicaris young*. Paratype male 3: A. urosome, dorsal view; B. urosome, lateral view. Paratype female 3: C. urosome, lateral view. Arabic numerals numbering sensilla consecutively from anterior to posterior end of body, and from dorsal to ventral side. Scales: 100μ m.



Fig. 28. *Proserpinicaris young*. Paratype male 3: A. antennula, ventral view; B. antenna, laterodorsal view; C. cutting edge of mandibula, anterior view; D. mandibula, postero-ventral view; E. maxillula, posterior view; F. maxilla, anterior view; G. maxilliped, anterior view. Paratype female 3: H. antennula, dorsal view. Scales: 50μ m.



Fig. 29. *Proserpinicaris young*. Paratype male 3: A. first swimming leg, anterior view; B. second swimming leg, anterior view; C. third swimming leg, anterior view; D. fourth swimming leg, anterior view. Paratype female 3: E. endopod of second swimming leg, posterior view; F. third swimming leg, anterior view; G. fourth swimming leg without last two exopodal segments, anterior view. Scales: 100 μ m.

guish from internal tissue and gut content; copulatory duct very short and weakly sclerotized. All posterior senislla homologous to those on male third urosomite, while two sensilla from male second urosomite missing (Nos. 32 and 34).

Third, fourth (preanal), and fifth (anal) urosomites very similar to male (Figs. 25B-D, 27C).

Caudal rami (Figs. 25B–D, 27C) slightly shorter in proportion to anal somite, about five times as long as wide in ventral (or dorsal) view, but also cylindrical and parallel or slightly divergent, with armature and ornamentation as in male.

Antennula (Figs. 25B, 28H) seven-segmented, ornamented on first segment with few minute spinules on ventral surface, not geniculate, with slender aesthetasc on fourth segment, not reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, which fused basally to two apical setae; proximal aesthetasc much more slender than in male; setal formula: 0.4.5.2.1.0.9. All setae, except proximalmost one on second segment, smooth, and most seta with pore on tip.

Antenna (Fig. 25B), labrum (Fig. 25F), paragnaths (Fig. 25F), mandibula (Fig. 25F), maxillula (Fig. 25F), maxilliped (Fig. 25F), first swimming leg, and second swimming leg (Fig. 29E) similar to male.

Third swimming leg (Fig. 29F) with smooth praecoxa and intercoxal sclerite. Coxa with arched row of large spinules on anterior surface, and two rows of spinules along distal margin on posterior surface, unarmed. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, which about as long as entire exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, linguiform, unarmed, reaching only 2/5 of first exopodal segment in length, ornamented with three small distal spinules.

Fourth swimming leg without spiniform process on basis. Endopod one-segmented, straight, ornamented with apical row of four spinules at base of apical spine and two spinules on inner margin; apical spine not distinct at base, smooth, and about 0.8 times as long as endopod; endopod with apical spine reaching posterior margin of first exopodal segment in length. Exopod similar to male, but inner margin of first exopodal segment lacks spinules.

Fifth leg (Figs. 25E, 27C) also simple cuticular plate, but without any spinules along inner margin and with longer row of minute spinules on posterior surface proximally. Armature same as in male.

Sixth legs vestigial (Fig. 25E), fused into simple cuticular flap, covering gonopores, unornamented and unarmed; distal margin thin, with produced lobe centrally and notches laterally.

TYPE LOCALITY: South Korea, Gyungsangbuk-do region, Sanggu city, Young River, interstitial from sandy beaches on banks, 36° 31′42.8″N 128° 14′02.7″E.

DISTRIBUTION: This species is only known from the type locality, Young River near Sanggu city, South Korea.

ECOLOGY: Specimens were obtained from interstitial on the river banks, but no data are available on the water chemistry or sediment grain size.

SPECIMEN EXAMINED: Types only: holotype male, allotype female, seven paratypes (three males and four females) together on 1 SEM stub (collection number NIBRIV0000232611); six paratypes (four males and two females) dissected on one slide each (collection numbers NIBRIV0000232612 to 0000232617); additional 36 paratypes (18 males, 11 females, and seven copepodids) together in alcohol (NIBRIV0000232618); 25 paratypes (10 males, 10 females, and five copepodids) sent for DNA barcoding; all collected from type locality, 24 April 2010, leg. J.-L. Cho, all deposited in the National Institute of Biological Resources, South Korea.

REMARKS: *Proserpinicaris young* is very closely related the Korean species *P. ondali*, as well as to two other Korean short-range endemics P. imjin and P. wangpi (see above). Their morphological differences are most related to the shape of the caudal rami, general habitus appearance, details in the shape of the fifth leg, as well as some other details of the ornamentation of the somites and armature of the antennulae, but they are not smaller than those between European members of this group, especially those from Italy and its islands, France, and Spain (see above). The easiest way to distinguish these Korean species is by the shape of their caudal rami. These are shortest in *P. imjin*, and even inflated in lateral view in females, resembling those of *P. phyllura* and some Italian populations of *P. proserpina*, although the latter may be a sign of an undescribed distinct species. The hypothesis about the caudal rami shape being a polymorphic character in parastenocaridids of Schminke (1991) was never challenged or seriously tested, especially not using molecular methods (Karanovic and Cooper 2011a, b). Proserpinicaris imjin also has a less vermiform habitus than any other Korean species, but its inner distal process on the male fifth leg is much longer and more robust than in other three species, showing that this difference is not a result of a single gene mutation (for example all appendages being elongated, or shortened). Proserpinicaris young, on the other hand, can be distinguished from other three Korean species by its exceptionally long caudal rami in both sexes, and also the apophysis of the male third leg is significantly shorter than the outer spine in this species. Proserpinicaris ondali and P. wangpi have the most similar shape of the caudal rami, but can be easily distinguished by the following five characters: P. ondali has a longer inner distal process on the male fifth leg, with the longest endopodal seta reaching only 1/2 of its length; the lateral setae on the caudal rami are inserted more posteriorly in P. ondali; caudal rami in male and female of about the same length or those of females even longer in *P. ondali*, whereas the female caudal rami are always significantly shorter than the male rami in P. wangpi: different armature formulas of male and female antennulae (although this may be a result of differing observations); and the anal somite with two short rows of spinules ventrally on the anterior half in P. ondali, whereas these are always missing in P. wangpi. In all three Korean species described by Karanovic et al. (2012) ventral spinules on the anal somite are missing. Recent combined morphological and molecular studies of short-range endemics from the genus Kinnecaris Jakobi, 1972 in Australia (Karanovic and Cooper 2011a), have shown that these morphological differences are good signs of separate biological species.

Key to the species of genus Proserpinicaris

1.	Hyaline process on the fourth leg basis in male significantly shorter than endopod2
-	This process as long as, or longer than endopod
2.	Inner margin of fourth leg endopod in male smooth distally
-	This margin plumose ······ P. cruzi
3.	Forth leg endopod extremely inflated in proximal half, wider than exopod P. nicolasi
-	Fourth leg endopod much more slender than exopod
4.	Third leg apophysis in male inflated distally P. hispanica
—	Apophysis wider in proximal than in distal half P. meridionalis
5.	Fourth leg endopod in male with crown of fused spinules, forming scoop-like structure 6
-	Endopod with pointed tip, without scoop-like structure
6.	Anal somite with two ventral rows of spinules7
-	Anal somite without ventral spinules
7.	Caudal rami more than six times as long as wide; dorsal caudal seta not longer than inner
	apical one ······ P. nipponensis

_	Caudal rami about five times as long as wide; dorsal caudal seta twice as long as inner apical
	one ····· P. ondali
8.	Female caudal rami leaf-like; male caudal rami slightly inflated posteriorly in ventral view P. imjin
_	Both female and male caudal rami cylindrical9
9.	Male caudal rami about six times as long as wide P. young
_	Male caudal rami about 4.3 times as long as wide P. wangpi
10.	Fourth leg endopod in male pinnate along inner margin P. cantabrica
_	Endopod not pinnate ······ 11
11.	Third leg exopodal spine in male inflated distally
-	This spine tapering distally
12.	Fourth leg endopod in male completely smooth and very slender P. ima
_	Endopod with serrated outer margin P. admete
13.	Fourth leg endopod in male serrated in proximal half, smooth distally P. kalypso
_	Endopod serrated in distal half 14
14.	Fourth leg endopod in male smooth proximally, serrated at least on one margin distally 15
_	Endopod with proximal half serrated at least on one side, or with tubercules 17
15.	Fourth leg endopod serrated along inner margin distally 16
_	Endopod serrated along outer margin distally P. gorganensis
16.	Caudal rami cylindrical P. pannonica
-	Caudal rami leaf-like P. phyllura
17.	Third leg in male with two prominent beaks on inner margin of first exopodal segment distally \cdots 18
_	This segment with smooth and concave inner margin distally 19
18.	Fourth leg endopod as long as basal hyaline process, lanceolate, with sharp tip P. amalasuntae
_	Endopod shorter than basal hyaline process, with minute slender seta apically P. proserpina
19.	Third leg apophysis in male very short, as wide as long; anal operculum with straight posterior
	margin P. mangini
_	Apophysis longer than wide; anal operculum very convex and long P. moravica

Genus Horstkurtcaris n. gen.

Type species: Parastenocaris nolli Kiefer, 1938.

OTHES SPECIES AND SUBSPECIES: *Parastenocaris delamarei* Chappuis, 1958; *Parastenocaris mangyans* Bruno and Cottarelli, 1999; *Parastenocaris nolli alpina* Kiefer, 1960; *Parastenocaris ursulae* Schminke, 1971.

ETYMOLOGY: The genus name is dedicated to Prof. Horst Kourt Schminke (Carl von Ossietzky University of Oldenburg, Germany), as a recognition of his contributon to our knowledge on the family Parastenocarididae. His first and middle names were prefixed to a Latin word for a crab (*caris*, *-idis*), originating from the Greek word of the same meaning ($k\alpha\rho_1\sigma$, $-i\delta_0\sigma$). Gender feminine.

DIAGNOSIS: Small to medium sized Parstenocaridinae (from 315 to 420 μ m), with cylindrical habitus, smooth cuticule, somites ornamted with few large sensilla, and with dorsal cuticular windows at least in some species. Podoplean boundary between prosome and urosome inconspicuous. Genital complex in female occupying anterior ventral half of genital double somite; genital apertures and

median copulatory pores covered by vestigial sixth legs, which fused completely into relatively narrow flap. Caudal rami cylindrical and long, with lateral cuticular pore near posterior margin, armed with seven elements (three lateral, one dorsal, and three apical) all situated in posterior part and often very close to posterior margin; lateral elements inserted close to each other and at about the same distance from anterior border as dorsal seta; one lateral element minute and hard to observe between two others. Male antennula seven-segmented, prehensile, with geniculation between third and fourth and fifth and sixth segments; last two segments in line; distal anterior corner of sixth (penultimate) segment without spiniform process, but spiniform process present on fourth segment on anterior surface; usually massive aesthetasc on fourth segment reaching tip of appendage. First swimming leg with inner basal armature element at least in two species. Second swimming leg with one-segmented endopod, armed with single slender seta apically, and with several apical spinules; no lateral spinules. Third swimming leg endopod in female very small and spiniform segment, probably armed with apical spine which fued basally to segment, smooth. Third swimming legs in male transformed into strong grasping organs, with large intercoxal sclerite between them, each composed of praexoca, coxa, basis, two-segmented exopod, and endopod reduced to single slender armature element; basis and proximal exopodal segment robust, latter usually with beaks or chitinous lobes on inner margin; outer spine on first exopodal segment smooth, large or small; ancestral distal exopodal segment (apophysis) well developed, usually conical, oriented slightly inwards, unornamented and unarmed, with blunt tip. Fourth swimming leg in male without spinules on inner margin of coxa, with single large and slender hyaline process (probably enlarged spinule) on inner margin of basis, and no other chitinous structures on basis; first exopodal segment with smooth and straight inner margin; endopod one-segmented and simple, usually spiniform and smooth (one species with more robust endopod ornamented with two subapical spinules on inner margin), without distinct apical armature, usually curved inwards. Fourth swimming leg in female without hyaline process on basis or inner spinules on first exopodal segment; endopod also onesegmented but cylindrical, straight, with strong element on tip, and several spinules at base of apical element. Fifth legs very similar in shape in male and female, elongated and simple triangular plates, with inner distal corner produced into short spiniform precess, with smooth and straight inner margin, and single large cuticular pore on anterior surface; armature inserted on outer margin and consists of very long outermost seta (ancestral basal), two setae at outer base of inner distal process (probably ancestral endopodal seta), and sometimes small seta (or long spinule?) at base of basal seta. Sixth legs in male also fused (or right one reduced and left one enlarged?) smooth, unarmed, unornamented, forming simple operculum covering gonopore.

REMARKS: Fourth swimming leg in male with a large and slender hyaline process on the inner margin of basis (probably enlarged spinule), being sole ornamentation on the inner half of basis, is a synapomorphy that unites all five species and subspecies included here in the genus *Horstkurtcaris* n. gen. All species also have a simple and invardly curved endopod of the fourth leg in male, but this character can be found in some other Parastenocaridinae genera, or species of *Parastenocaris* Kessler, 1913 that are currently considered to be members incertae sedis of this subfamily by Schminke (2010) (see the Introduction section above). Other features that distinguish the newly erected genus are long and cylindical caudal rami, with lateral and dorsal setae in the same plane (in some very close to posterior margin), last two antennular segments in male in line, penultimate segment of the male antennula without spiniform process, basis of the first leg with inner element, endopod of the third leg in female spiniform and smooth, similar shape, armature and ornamentation of the male third leg, and similar shape and armature of the fifth leg in both sexes. While some of these feaures are undoubtedly plesiomorphic character states (inner basal element on the first leg), and

others may have originated convergently in other groups (and thus are homoplastic characters in a wider group), we are convinced that most of them are synapomorphies of this group, and thus a proof that they shared a common ancestor that was not ancestral to any other currently known (and sufficiently illustrated) parastenocaridid.

Jakobi (1972) considered *Parastenocaris nolli* and *P. delamarei* as members of the genus *Proserpinicaris*, but Karanovic et al. (2012) argued against this in their redefinition of the genus. For example, *P. nolli* has its lateral caudal setae inserted near posterior margin, very short fifth legs both in male and female, and relatively small spinules on the male fourth leg basis inserted medially from endopod, among many morphological differences (see Kiefer, 1938, 1960a, b), and it was placed in the nomino-typical subfamily by Schminke (2010). *Parastenocaris delamarei* was also placed in the nomynotypical subfamily by Schminke (2010), and it differs from all 20 species of *Proserpinicaris* by the shape of the male third leg, armature of the male fourth leg basis, and insertion of lateral setae on the caudal rami (see Chappuis, 1958). Here we designate a new genus for these two former memners of the *proserpina* group, where we also include one subspecies of *P. nolli* (*P. nolli alipna*) and two other species: *P. mangyans* and *P. ursulae* (see above). They were also considered incertae sedis in the subfamily Parastenocaridinae by Schminke (2010). The genus *Horstkurtcaris* n. gen., although not speciose, has a very wide distribution, with is members reported from Germany, Canada, Canary Islands, and the Philippines. We expect that many more members are awaiting to be discovered and described, especially in poorely surveyed regions of Asia and North America.

21. *Horstkurtcaris delamarei* (Chappuis, 1958 in Chappuis and Delamare Deboutteville, 1958) n. comb. (Fig. 30)

Parastenocaris delamarei Chappuis: in Chappuis and Delamare Debouteville, 1958, p. 372, fig. 4/8–11; Chappuis, 1958, p. 426, fig. 2.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 350 μ m. Colour, nauplius eye, ornamentation of somites, and presence/absence of cuticular windows also unknown, but probably similar to type species.

Anal somite (Fig. 30A) unornamented, quite elongated. Anal operculum well developed, unornamented on outer surface, with almost straight distal margin, almost reaching posterior end of anal somite.

Caudal rami (Fig. 30A) about three times as long as greatest width (dorsal view) and about 0.6 times as long as anal somite, unornamented, cylindrical but slightly swollen in central part (at least in ventral view), divergent, with space between them about 1.5 ramus width; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta of unknown length. Both lateral setae short and smooth, of about same length, 0.4 times as long as ramus, inserted close to each other at 3/4 of ramus length. Inner apical seta slender and smooth, inserted more ventrally, about half times as long as ramus; insertion on outer edge of ramus (Fig. 30A) either erroneous or ramus twisted during slide preparation. Middle apical seta strongest, without breaking plane, smooth, much longer than caudal ramus; exact length unknown. Outer apical seta also relatively strong and smooth, but only about as long as caudal ramus.

Antennula, antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, and second



Fig. 30. *Horstkurtcaris delamarei*, Male. A. anal somite and left caudal ramus, ventral view; B. third swimming leg; C. fourth swimming leg; D. fifth leg. Scales: unknown (cited from Chappuis and Delamare Deboutteville, 1958, modified).

swimming leg unknown but probably similar to type species.

Third swimming leg (Fig. 30B) with smooth praecoxa, coxa, and intercoxal sclerite. Basis mot very robust and partly fused to coxa, armed with strong outer seta, ornamented with diagonal row of large spinules close to outer margin. Endopod absent. Exopod with both segments fused; ancestral proximal segment four times as long as wide, oriented inwards, with small beak on inner margin proximally, but with slightly concave inner margin, ornamented with two rows of large spinules on outer margin, armed subapically with very small but strong, smooth blunt spine, much shorter than apophysis, and points outwards; ancestral distal segment (apophysis) spiniform, long, smooth, unornamented and unarmed, pointing inwards.

Fourth swimming leg (Fig. 30C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis ornamented with large chitinous inwards-pointing spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta almost as long as entire exopod and more than twice as long as outer spine. Endopod very reduced, one-segmented and spiniform, much shorter than basal spiniform process, unornamented, straight and pointing distally.

Fifth leg (Fig. 30D) simple triangular cuticular plate, three times as long as wide, inner distal corner produced into short and smooth spiniform process, unornamented, armed with three smooth setae; outermost seta (ancestral basal one) longest, half as long as entire leg, and 1.8 times as long as other two setae (ancestral endopodal), which are subequal. Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown.

Female: Body length, habitus shape, colour and somite ornamentation unknown, but probably very similar to male, except genital and first abdominal somite fused into double somite. Anal somite, anal operculum, and caudal rami similar to male. Most other characters unknown, but probably similar to type species.

TYPE: Type material probably lost.

TYPE LOCALITY: Canada, Ontario, Lake Erie, Turkey Point, interstitial from lake beach.

DISTRIBUTION: This species is only known from the type locality, a beach on Lake Erie at Turkey Point, Canada.

ECOLOGY: It seems that *H. delamarei* is also a classic interstitial species, specialised for life in fine sands of lake shores.

REMARKS: Chappuis and Delamare Deboutteville (1958) did not discuss the affinities of the new species, but it is fairly clear that it shares some morphological characters with *H. nolli nolli* and *H. nolli alpina*, especially in the shape and armature of the male third and fourth legs. It can be distinguished from both by a much longer apophysis and absent endopod on the male third leg (Fig. 30B), as well as by somewhat shorter caudal rami (Fig. 30A). Unfortunately, the original description is lacking in detail and many morphological characters could not be compared. Chappuis (1958) did not provide any additional information, but only reproduced the drawing on the male fourth leg from his previous publication (Chappuis and Delamare Deboutteville, 1958).

22. Horstkurtcaris mangyans (Bruno and Cottarelli, 1999) n. comb. (Fig. 31)

Parastenocaris mangyans Bruno and Cottarelli, 1999, p. 511, figs. 1-3, 10, 11.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 315 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width difficult to establish. Body length/width ratio about 7.2; cephalothorax about as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites. Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax about 1.5 times as long as wide in dorsal view; representing 20% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally very sparse.

Urosomal somites (except preanal, unornamented) with six posterior sensilla and with smooth hyaline fringes.

Anal somite (Fig. 31A) ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with concave and smooth distal margin, not reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, one of on internal margin of anal operculum basally.

Caudal rami (Fig. 31A) about three times as long as greatest width (dorsal view) and only slightly shorter than anal somite, tapering towards distal end and with slightly produced dorsal distal corners, divergent, with space between them about one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore near posterior margin dorsolaterally and two small spinules near posterior margin ventrally. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/5, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other and also at 3/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.8 times as long as ramus, and about five times as long as other two setae, which are subequal and minute. Inner apical seta small, smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth, length unknown. Outer apical seta also without breaking plane and smooth, but much more reduced in size and strength, only about 0.7 times as long as ramus.

Antennula (Fig. 31B) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment not reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (possibly incomplete): 0.6.5.2.0.0.8. Most setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 31C) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 3.5 times as long as wide, unarmed, unornamented. Endopod about 0.6 times as long as allobasis and 2.4 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single small apical seta, twice as long as segment.

Mandibula (Fig. 31D) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 31E) with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements

(probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 31F) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with only one endite, armed with one smooth and one pinnate seta apically. Basis drawn out into strong and pinnate claw, probably without seta at base (although drawn on original line drawings; not seen on SEM photos). Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 31G) with very short but strong syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and twice as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 31H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch on inner margin, and armed with single short seta on outer margin and with long thin seta near inner margin at base of endopod. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.4 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 311) with smooth praecoxa, and intercoxal sclerite. Coxa with posterior row of minute spinules. Basis armed with outer seta, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.1 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about eight times as long as wide, not reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing inwards.

Third swimming leg (Fig. 31J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin; additional long row of minute spinules on inner margin. Endopod minute but distinct segment, curved, about as long as largest spinule on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment 4.5 times as long as wide, curved inwards and with smooth inner margin, ornamented with several spinules on outer margin basally and few more distally, armed subapically with complex, strong, smooth and short spine, significantly shorter than apophysis and curved outwards; ancestral distal segment (apophysis) also short and complex tridimensional structure, somewhat conical, oriented outwards, unornamented and unarmed.

Fourth swimming leg (Fig. 31K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge chitinous spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner



Fig. 31. *Horstkurtcaris mangyans*. Male: A. last two urosomal somites and caudal rami, dorsal view; B. antennula; C. antenna; D. mandibula; E. maxillula; F. maxilla; G. maxilliped; H. first swimming leg; I. second swimming leg; J. third swimming leg; K. fourth swimming leg; L. fifth leg. Female: M. basis and first endopodal and exopodal segments of first swimming leg; N. second swimming leg without last two exopodal segments; O. third swimming leg; P. fourth swimming leg without last two exopodal segments; Q. fifth legs. Scales: 25 μ m (cited from Bruno and Cottarelli, 1999, modified).

side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.7 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, smooth, very simple structure, without armature (except maybe fused apical smooth spine) or ornamentation.

Fifth leg (Fig. 31L) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, ornamented with single spinule near base of outermost seta, armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.25 times as long as entire leg; middle seta (ancestral outer endopodal) 0.7 times as long as leg, and 1.25 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 320 μ m in one paratype. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite slightly longer than wide (dorsal view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites), plus additional cuticular window ventrally in posterior half. Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami very similar to male, and only slightly shorter in proportion to anal somite and with somewhat more slender anterior part.

Antennula also seven-segmented but not geniculate, unornamented, armature similar to male.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 31M), second swimming leg (Fig. 31N), and exopod of fourth swimming leg (Fig. 31P) similar to male.

Third swimming leg (Fig. 31O) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, smooth and spiniform, reaching to 2/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 31P) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, and about half as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 31Q) also simple cuticular plate, but more elongated; inner distal corner produced posteriorly as in male. Armature same as in male. Only ornamentation consists of large cuticular pore basally on anterior surface.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap.

TYPE: The holotype male and one paratype female were deposited in the Museo Civico di Storia

Naturale "G. Doria" in Genova; the rest of the type material is deposited in the second author's working collection in the Dipartimento di Scienze Ambientali, Università della Tuscia, Viterbo.

TYPE LOCALITY: Philippines, Mindoro Island, Talipanan village, interstitial of a freshwater stream. **DISTRIBUTION:** This species is known from the type locality, the hyporheic of a freshwater stream near Talipanan village, and from a well near Sabang village, both on Mindoro Island, Philippines.

ECOLOGY: Specimens were obtained from a well and from hyporheic habitats next to a fast-flowing stream. As most other members of the family Parastenocarididae Chappuis, 1940, this species is also an interstitial form.

REMARKS: *Horstkurtcaris mangyans* differs from all other parastenocaridids by the presence of ventral cuticular window on the genital double somite, which was illustrated by Bruno and Cottarelli (1999), but unfortunately not supported by SEM evidence, although they made an extensive collection of SEM images (it is possible that this structure is internal). They noted that the shape of the fourth leg in male is relatively similar to that in *H. nolli* but did not provide distinguishing morphological features. The third leg in the male differs considerably between these two species, as do the caudal rami in both sexes.

23. Horstkurtcaris nolli alpina (Kiefer, 1960) n. comb. (Fig. 32)

Parastenocaris nolli alpina Kiefer, 1960b, p. 38, figs. 1–12. [partim.] *Parastenocaris nolli* Kiefer: Dussart, 1967, p. 420, fig. 186.

Male: Total body length unknown, but probably similar to nominotypical subspecies. Colour, nauplius eye, ornamentation of somites, and presence/absence of cuticular windows also unknown, but probably similar to nominotypical subspecies.

Anal somite (Fig. 32A) ornamented with pair of large dorsal sensilla at base of anal operculum, transverse ventral row of large spinules at first third, and with several minute spinules along posterior margin ventrally, at base of caudal rami. Anal operculum well developed, unornamented on outer surface, with almost straight distal margin, almost reaching posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened, ornamented with many rows of slender spinules, one of them along ventral surface of anal somite.

Caudal rami (Fig. 32A) about five times as long as greatest width (dorsal view) and about 1.25 times as long as anal somite, cylindrical and only tapering posteriorly in last sixth, divergent, with space between them about 1.5 ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of few ventral spinules on posterior margin. Dorsal seta slender and smooth, inserted close to inner margin at about 5/6, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other also at 5/6 of ramus length. Proximal lateral seta placed more dorsally, 0.3 times as long as ramus, and more than twice as long as middle seta, minute; about as long as distal lateral seta. Inner apical seta slender and smooth, inserted more ventrally, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, 2.5 times as long as caudal ramus. Outer apical seta also very small and slender, only about as long as longer lateral setae.

Antennula (Fig. 32B) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process,

but fourth segment with small spiniform process basally on anterior surface. Very wide and long aesthetasc on fourth segment, reaching beyond tip of appendage. Much shorter and more slender apical aesthetasc on seventh segment. Setal formula (probably incomplete) 0.6.1.3.1.0.8.

Antenna, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown but probably similar to nominotypical subspecies.

Second swimming leg (Fig. 32C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about six times as long as wide but only reaching midlength of first exopodal segment in length, ornamented with four large spinules along apical margin; armed apically with one smooth seta, about as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 32D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta, ornamented with diagonal row of large spinules close to outer margin. Endopod reduced to slender seta, about twice as long as spinules on outer margin but stronger, unornamented. Exopod with both segments fused; ancestral proximal segment 4.4 times as long as wide, oriented inwards, with small beak on inner margin proximally, but with concave inner margin, ornamented with two rows of large spinules on outer margin, armed subapically with simple, strong, smooth and sharp spine, somewhat longer than apophysis, and pointing outwards; ancestral distal segment (apophysis) thumb-like, relatively short, unornamented and unarmed, with inner distal corner produced into spiniform process (probably fused ancestral apical spine).

Fourth swimming leg (Fig. 32E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with several small spinules on outer margin and large chitinous inwards-pointing spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta almost as long as entire exopod and more than twice as long as outer spine. Endopod very reduced, one-segmented and spiniform, much shorter than basal spiniform process, unornamented, curved and pointing inwards.

Fifth leg (Fig. 32F) simple triangular cuticular plate, three times as long as wide, inner distal corner produced into short and smooth spiniform process, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, 1.2 times as long as entire leg; next seta (probably ancestral exopodal) only 0.24 times as long as leg; third seta (ancestral outer endopodal) 0.5 times as long as leg, and twice as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, habitus shape, colour, and somite ornamentation unknown, but probably very similar to male, except genital and first abdominal somite fused into double somite. Caudal rami (Fig. 32G) very similar to male, but with slightly longer proximal lateral seta and slightly shorter innermost apical one, although this may be result of intraspecific variability rather than sexual dimorphism.

Antennula (Fig. 32H) also seven-segmented but not geniculate, with slender aesthetasc on fourth



Fig. 32. *Horstkurtcaris nolli alpina*. Male: A. anal somite and left caudal ramus, dorsal view; B. antennula; C. second swimming leg; D. third swimming leg; E. fourth swimming leg; F. fifth leg. Female: G. anal somite and right caudal ramus, ventral view; H. antennula; I. second swimming leg without last two exopodal segments; J. third swimming leg without last two exopodal segments; K. fourth swimming leg without last two exopodal segments; L. fifth leg. Scales: 50 μ m (cited from Kiefer, 1960b, modified).

segment, hardly reaching tip of appendage, and somewhat shorter apical aesthetasc on seventh segment, fused basally to at least one apical seta; both aesthetascs much more slender than in male; setal formula (probably incomplete): 0.4.3.1.0.1.5.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming (Fig. 32I), and exopod of fourth swimming leg (Fig. 32K) similar to male.

Third swimming leg (Fig. 32J) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with few spinules on outer margin, armed with very long and smooth outer seta. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, spiniform, unarmed and unornamented, reaching 2/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 32K) without spiniform process on basis. Endopod one-segmented, cylindrical, ornamented with four spinules at base of apical spine, partly fused at base, smooth, 0.7 times as long as endopod; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 32L) also simple cuticular plate, but somewhat more elongated in distal part, also without spinules along inner margin. Armature same as in male, but distance between single exopodal seta and two endopodal setae more pronounced.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: Type material in the Kiefer Collection, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

TYPE LOCALITY: Germany, southern Bavaria, Garmisch-Partenkirchen district, Mittenwald town, well.

DISTRIBUTION: This species is only known from the type locality, a well in Mittenwald in southern Germany.

ECOLOGY: It seems that *H. nolli alpina* is also a classic interstitial species, specialised for life in fine sand in alluvial plains, but in smaller rivers and at higher altitudes. This would imply its preference for colder water during European summers, which may be one of the important ecological factors that contributes towards the reduction of gene flow between it and the nominotypical subspecies, and maintaining of morphological differences.

REMARKS: Kiefer (1960) pointed out ventral ornamentation of the anal somite in female, as well as the reduced size of the outer apical seta on the caudal rami in both sexes, as the main morphological differences between the two subspecies, in addition to a less-rounded anal operculum. In our experience these are indicative of species-level taxa, but without examining any material and also without molecular data, we prefer to leave these as two subspecies. Dussart (1967) considered *H. nolli alpina* to be a synonym of *H. nolli nolli*, a view that we certainly do not share.

24. Horstkurtcaris nolli nolli (Kiefer, 1938) n. comb. (Fig. 33)

Parastenocaris nolli Kiefer, 1938, p. 144, figs. 1–14; Lang, 1948, p. 1245, fig. 500-2; [partim.] Dussart, 1967, p. 420, fig. 186.

Parastenocaris nolli nolli Kiefer, 1960a, p. 326, figs. 18-23.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 420 μ m. Preserved specimen probably colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Ornamentation of somites and presence/absence of cuticular windows unknown.

Anal somite (Fig. 33A, B) ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 80% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 33A, B) about five times as long as greatest width (dorsal view) and about 1.25 times as long as anal somite, cylindrical and only tapering posteriorly in last sixth, divergent, with space between them about 1.5 ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of few ventral spinule on posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6, about as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other also at 5/6 of ramus length. Proximal lateral seta placed more dorsally, 0.4 times as long as ramus, and more than twice as long as other two lateral setae, minute. Inner apical seta slender and smooth, inserted more ventrally, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, 2.5 times as long as caudal ramus. Outer apical seta also without breaking plane but unipinnate, relatively strong basally, much more slender and shorter, only about 0.6 times as long as caudal ramus.

Antennula (Fig. 33C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Very wide and long aesthetasc on fourth segment, reaching beyond tip of appendage. Much shorter and more slender apical aesthetasc on seventh segment. Setal formula unknown.

Antennula, antenna, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown but probably similar to type species.

Second swimming leg (Fig. 33D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis also unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about 7.6 times as long as wide but not reaching midlength of first exopodal segment in length, ornamented with four large spinules along apical margin; armed apically with one smooth seta, about 0.6 times as long as segment and pointing slightly inwards.

Third swimming leg (Fig. 33E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta, ornamented with diagonal row of large spinules close to outer margin. Endopod reduced to slender seta, about twice as long as spinules on outer margin but stronger,

unornamented. Exopod with both segments fused; ancestral proximal segment 4.4 times as long as wide, oriented inwards, with small beak on inner margin proximally, but with concave inner margin, ornamented with two rows of large spinules on outer margin, armed subapically with simple, strong, smooth and sharp spine, somewhat longer than apophysis, and pointing outwards; ancestral distal segment (apophysis) thumb-like, relatively short, unornamented and armed, with inner distal corner produced into spiniform process (probably fused ancestral apical spine).

Fourth swimming leg (Fig. 33F) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with large chitinous inwards-pointing spiniform process between exopod and endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta as long as entire exopod and more than twice as long as outer spine. Endopod very reduced, one-segmented and spiniform, much shorter than basal spiniform process, unornamented, curved and pointing inwards.

Fifth leg (Fig. 33G) simple triangular cuticular plate, three times as long as wide, inner distal corner produced into short and smooth spiniform process, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, 1.2 times as long as entire leg; next seta (probably ancestral exopodal) only 0.24 times as long as leg; third seta (ancestral outer endopodal) 0.5 times as long as leg, and twice as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 420 μ m. Habitus (Fig. 33H), ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite (Fig. 33I, J) and habitus slightly less slender. Caudal rami (Fig. 33I, J) very similar to male.

Antennula (Fig. 33K) also seven-segmented but not geniculate, with slender aesthetasc on fourth segment, hardly reaching tip of appendage, and somewhat shorter apical aesthetasc on seventh segment, fused basally to at least one apical seta; both aesthetascs much more slender than in male; setal formula unknown.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming (Fig. 33L), and exopod of fourth swimming leg (Fig. 33N) similar to male.

Third swimming leg (Fig. 33M) with large praecoxa, smooth coxa and intercoxal sclerite. Basis unornamented, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, spiniform, unarmed and unornamented, reaching only 2/3 of first exopodal segment in length.

Fourth swimming leg (Fig. 33N) without spiniform process on basis. Endopod one-segmented, spiniform, unornamented, armed with smooth apical spine, fused at base; endopod with apical spine not reaching posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 33O) also simple cuticular plate, but somewhat wider and shorter, also without spinules along inner margin. Armature probably same as in male, although drawn with only three setae.

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced



Fig. 33. *Horstkurtcaris nolli nolli*. Male: A. last two urosomal somites and caudal rami, dorsal view; B. anal somite and right caudal ramus, ventral view; C. distal part of antennula without armature; D. second swimming leg without last two exopodal segments; E. third swimming leg; F. fourth swimming leg without last two exopodal segments; G. fifth leg. Female: H. habitus, dorsal view; I. urosome, dorsal view; J. urosome, lateral view; K. antennula without armature; L. endopod and first exopodal segment of second swimming leg; M. endopod and first exopodal segment of third swimming leg; N. endopod and first exopodal segment of fourth swimming leg; O. fifth leg. Scales: A, F–O=unknown, B–G=50 μ m (cited from Kiefer, 1938, 1960a, modified).

into small spiniform process.

TYPE: Type material in the Kiefer Collection, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

TYPE LOCALITY: Germany, northwestern Bavaria, Aschaffenburg, well in Schönbusch Park.

DISTRIBUTION: Besides the type locality, a well in Aschaffenburg, Germany, this species was reported by Kiefer (1960a) from several other unspecified localities. It seems that the species may be distributed more widely in the River Main alluvial plain, in the southwestern part of Germany. Kiefer (1960b) summarised records of other scientists, but those would be difficult to verify as they are part of either ecological studies or PhD theses. In both cases identifications were done by people who were not taxonomic experts.

ECOLOGY: It seems that *H. nolli nolli* is a classic interstitial species, specialised for life in fine sand in alluvial plains of large European rivers. Kiefer (1960a) promised that S. Husmann, who collected material for his study, would publish environmental data separately at a later stage. Unfortunately, to our knowledge, this information never appeared in the scientific literature.

REMARKS: Kiefer (1938) did not discuss affinities of his new species. Lang (1948) assigned it to the *proserpina* group, considering the shape and armature of the fourth leg endopod in the male. Rouch (1992) considered this group as probably polyphyletic, and noted that *H. nolli* stands well apart from *P. proserpina* and other closely related species. Although the original species description is lacking in detail, and we have not examined any material ourselves, there seems to be enough information available to make us question the position of this species in the genus *Proserpinicaris*. The caudal rami shape and armature, as well as the armature and ornamentation of the fourth leg in the male, suggest an isolated position of *H. nolli nolli* in the family, closely related only to *H. nolli alpina* (see above). Thus we proposed a new genus to accommodate these two taxa, with several other more or less closely related species.

25. Horstkurtcaris ursulae (Schminke, 1971) n. comb. (Fig. 34)

Parastenocaris ursulae Schminke, 1971, p. 71, figs. 4, 5.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 398 μ m in holotype. Preserved specimen colourless. Nauplius eye absent. Body about nine times as long as wide, composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome. No information available on somite ornamentation, but dorsal cuticular window on cephalothorax absent and no cuticular windows on other somites reported.

Anal somite (Fig. 34A, B) only slightly longer than preanal somite, ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with almost straight and smooth distal margin, reaching posterior end of anal somite, representing 75% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules, one of on internal margin of anal operculum basally.

Caudal rami (Fig. 34A, B) about four times as long as greatest width (dorsal view) and about as

long as anal somite, cylindrical, slightly convergent, with space between them about one ramus width, unornamented; armed with six armature elements (two lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 5/6, about slightly longer than caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other at 5/6 of ramus length. Proximalmost lateral seta placed more dorsally, 0.36 times as long as ramus, and 1.5 times as long as distal seta. Inner apical seta small, smooth, inserted more ventrally, about half as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about five times as long as ramus. Outer apical seta also without breaking plane and relatively strong basally but much shorter, about 0.7 times as long as caudal ramus.

Antennula (Fig. 34C) relatively long, seven-segmented, prehensile and digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment not produced into spiniform process. Slender aesthetasc on fourth segment slightly reaching beyond tip of appendage, fused basally to equally long seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.5.2.3.0.0.8. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 34D) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 3.5 times as long as wide, unarmed and unornamented. Endopod about 0.6 times as long as allobasis and 2.2 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, twice as long as segment.

Mandibula, maxillula, maxilla, and maxilliped unknown but probably similar to type species.

First swimming leg (Fig. 34E) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another one on inner margin, and armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and only slightly longer than larger geniculate exopodal seta.

Second swimming leg (Fig. 34F) with smooth praecoxa, coxa, and intercoxal sclerite. Basis ornamented with row of spinules on outer margin, unarmed. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.1 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical, about five times as long as wide, reaching midlength of first exopodal segment, ornamented with and several large spinules along apical margin; armed apically with one smooth seta, about 0.4 times as long as segment.

Third swimming leg (Fig. 34G) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row large spinules near outer margin

distally. Endopod small, spiniform, and smooth. Exopod with both segments fused; ancestral proximal segment 3.2 times as long as wide, curved inwards, and with two small chitinous beaks on inner margin proximally, ornamented with large spinules on outer margin proximally and distally; armed subapically with strong smooth spine, significantly longer than apophysis and curved inwards; ancestral distal segment (apophysis) spiniform but stronger than spine, also oriented inwards, short and smooth.

Fourth swimming leg (Fig. 34H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis armed with single outer seta, ornamented with diagonal row of large spinules near outer margin and huge chitinous spiniform process between exopod and endopod, curved inwards and appears to be further ornamented with two apical hairs. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 1.2 times as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented and spiniform, smooth, curved outwards.

Fifth leg (Fig. 34I) simple triangular cuticular plate, inner distal corner produced into short smooth spiniform process, nearly three times as long as greatest width, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; next seta (ancestral exopodal) very small, almost like a spinule; third seta from outer side (ancestral outer endopodal) 0.6 times as long as leg, and about 1.6 times as long as innermost seta (ancestral inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs unknown, but probably smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, 385 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite. Other information on shape and ornamentation of somites missing.

Caudal rami very similar to male.

Antennula (Fig. 34J) also seven-segmented but not geniculate, unornamented, with slender aesthetasc on fourth segment, reaching slightly beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (probably incomplete): 0.4.3.2.0.0.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 34L) similar to male.

Third swimming leg (Fig. 34K) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, longer than entire exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, small, spiniform, unornamented, probably armed apically with single spine basally fused to somite.

Fourth swimming leg (Fig. 34L) without spiniform process on basis. Endopod one-segmented, ornamented with transverse apical row of four spinules at base of apical spine, distinct at base, unipinnate, and about 0.7 times as long as endopod; endopod with apical spine reaching beyond posterior margin of first exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 34M) also simple cuticular plate, but slightly narrower than on male. Armature and ornamentation same as in male, except outer exopodal seta proportionately shorter.



Fig. 34. *Horstkurtcaris ursulae*. Male: A. anal somite and right caudal ramus, lateral view; B. anal somite and caudal rami, dorsal view; C. antennula; D. antenna; E. first swimming leg; F. second swimming leg; G. third swimming leg; H. fourth swimming leg; I. fifth leg. Female: J. antennula; K. third swimming leg; L. fourth swimming leg; M. fifth leg. Scales: 50 μ m (cited from Schminke, 1971, modified).

Sixth legs unknown, but probably vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed, mostly fused, forming single bilobate flap, with outer distal corner produced into small spiniform process.

TYPE: The type material is deposited in the author's private working collection in Oldenburg, Germany.

TYPE LOCALITY: Canary Islands (Spain), Tenerife, Adeje, Barranco del Infierno stream, interstitial.

DISTRIBUTION: This species is known only from the type locality, Barranco del Infierno stream in Tenerife, Canary Islands (Spain).

ECOLOGY: Very little information was provided about the type locality and environmental conditions, but it is clear that specimens were collected from interstitial sediments in Barranco del Infierno, a very deep ravine with a temporary stream and many waterfalls. The island of Tenerife is volcanic in origin, which poses interesting questions about the colonisation of subterranean freshwater organisms such as parastenocaridids (Schminke, 1971). We suggest that anthropogenic translocation associated with early shipping activities may be one of the possible explanations (see Karanovic and Krajicek 2012), which would imply that this species may have its original population somewhere else still undiscovered.

REMARKS: Schminke (1971) considered his *H. ursulae* to be a member of the *proserpina* group, and morphologically most similar to *P. cantabrica*, but he observed enough morphological differences in the shape and ornamentation of the swimming legs and caudal rami to be able to justify a new species. In our view, the species really has no close relatives among living congeners, and can be distinguished by many morphological characters. It differs from *P. cantabrica* by many characters, such as the position of lateral setae on the caudal rami, as well as the curved endopod of the fourth leg in male. Schminke (2010) placed *H. ursulae* as incertae sedis in the subfamily Parastenocaridinae.

Key to the species of genus Horstkurtcaris

1.	Outer spine on male third leg exopod as long as apophysis 2
—	This element much smaller than apophysis H. delamarei
2.	All caudal armature inserted very close to posterior margin
—	Caudal armature inserted at 3/5 of caudal rami H. mangyans
3.	Endopod of male fourth leg spiniform and smooth
-	This segment more robust distally and with two inner spinules
4.	Outer apical caudal seta robust and longer than any later caudal seta
_	This seta minute

Genus Parastenocaris Kessler, 1913

The brevipes group

REMARKS: Reid (1995) reviewed this group of species, while redescribing *Parastenocaris brevipes* Kessler, 1913 from numerous localities in the Holartcic and synonymizing several previously described

species with it, as well as the genus Biwaecaris Jakobi, 1972 with Parastenocaris Kessler, 1913. She also provided a list of morphological characters to define this group and included in it the following 11 species (besides P. brevipes): P. arctica Bortuzky, 1952; P. brincki Enckell, 1970; P. feuerborni Chappuis, 1931; P. hinumaensis Kikuchi, 1970; P. irenae Enckell, 1970; P. lanceolata Enckell, 1970; P. longicaudis Chappuis, 1931; P. longipoda Shen and Tai, 1973; P. noodti Enckell, 1970, P. oshimaensis Miura, 1962; P. singhalensis Enckell, 1970. Karanovic (2005a, 2006) argued that P. arctica and P. longicaudis cannot be confidently included in this group for the lack of males. In this paper we argue for a separate status of P. biwae Miura, 1969, which was synonymized with P. brevipes by Reid (1995), and for the inclussion of *P. palmerae* Reid, 1991, which was not considered a member of this group by the same author. Karanovic and Lee (2012) described one new species from Korea, and included in this group four other species described subsequently: P. gayatri Ranga Reddy, 2001; P. jane Karanovic, 2006; P. kimberleyensis Karanovic, 2005, and *P. savita* Ranga Reddy, 2001. This group of species contains the type species of the genus Parastenocaris (P. brevipes) and cannot be separated from the bulk of species nomenclaturally without a proper revision of the whole family. Gallassi and Laurentiis (2004) repeated the major points of the review done by Reid (1995), and tried to subdivide the huge genus Parastenocaris by calling the brevipes group Parastenocaris s. str., which is meaningless nomenclaturally. As groups of species are not recognized nomeclatural categories either (ICZN, 1999), we are not providing the diagnosis here, but instead just list recognised species alphabetically below. Most taxonomists today agree that this will be the revised genus *Parastenocris*, once all other species are separated into different genera (Corgosinho et al., 2007, 2008; Schminke, 2008, 2010; Ranga Reddy and Defaye, 2009; Karanovic and Cooper, 2011a, b; Karanovic et al., 2012).

26. *Parastenocaris biwae* Miura, 1969 (Figs. 35–37)

Parastenocaris biwae Miura, 1969, p. 40, figs. 1–15; Dussart and Defaye, 1990, p. 254; Karanovic and Lee, 2012.

Parastenocaris brevipes Kessler, 1913: Reid, 1995, p. 177, fig. 2i.

Male: (based on two newly collected specimens). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 600 to 612 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites (first pedigerous fused to cephalothorax)), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Podoplean boundary between prosome and urosome inconspicuous. Habitus (Fig. 35A) cylindrical and very slender, without any demarcation between prosome and urosome; prosome/urosome ratio about 0.8 in dorsal view; greatest width in dorsal view at posterior end of cephalothorax but hard to establish (fourth pedigerous somites only slightly narrower); free prosomal somites in lateral view as wide as cephalothorax or urosome. Body length/width ratio about 9.1; cephalothorax 1.1 times as wide as genital somite. Free pedigerous somites without any lateral or dorsal expansions, all connected by well developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes, especially dorsally, except in preanal somite, where hyaline fringe well developed (Fig. 35A). Integument weakly sclerotized, smooth but covered with shallow pits on all somites and caudal rami, ornamented only with sensilla and pores (no spinules, except on posterior margin of caudal rami ventrally), with round dorsal double cuticular window

on cephalothorax, trapezoidal simple dorsal cuticular window on genital, and elongated simple dorsal windows on three postgenital somites (Fig. 35A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view.

Rostrum (Fig. 35A) small, membranous, not demarcated at base, ornamented with two large dorsal sensilla (No. 1), linguiform but with pointed tip, hardly reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax (Fig. 35A, C) about 1.8 times as long as wide in dorsal view; representing 20% of total body length. Surface of cephalic shield ornamented with 16 pairs of large sensilla (all homologous with sensilla in *P. young* and assigned same Arabic numerals); with a dense pattern of cutical pits of different sizes; five pairs of sensilla surround double cuticular window, but its surface completely smooth. Athroidal membrane between cephalothorax and second pedigeous somite (first free) wider than between any other somites.

Second pedigerous somite (Fig. 35A) slightly narrower than posterior half of cephalothorax in dorsal view, with four pairs of large sensilla (three dorsal and one lateral; Nos. 17–20), and with unpaired dorsal pore in anterior half.

Third pedigerous somite (Fig. 35A) slightly wider and shorter than second pedigerous, with four pairs of large sensilla (Nos. 21–23 and 25), also with unpaired dorsal pore; note: sensilla pair No. 24 missing (present in *P. young*).

Foruth pedigerous somite (Fig. 35A) widest and longest free prosomal somite in dorsal view, with only three pairs of large posterior sensilla (Nos. 26–28), with arched sutures in anterior part dorsally and unpaired cuticular pore in between them.

First urosomite (= fifth pedigerous somite) (Fig. 35A) slightly narrower and shorter than fourth pedigerous somite, also with three pairs of large posterior sensilla (Nos. 29–31), without arched dorsal sutures or cuticular pores.

Second urosomite (= genital somite) (Fig. 35A, D) slightly narrower and longer than first urosomite, about 1.2 times as wide as long in ventral view, with trapezoidal small cuticular window in anterior half, also with three pairs of posterior sensilla (Nos. 32–34), but dorsal pair (No. 32) closer to each other than in first urosomite; single longitudinally placed spermatophore inside longer than somite.

Third urosomite (Figs. 35A,) about as long as second urosomite but slightly narrower, with shorter but much wider dorsal cuticular window, and with three pairs of large posterior sensilla (Nos. 36, 37 and 39); sensilla Nos. 35 and 38 missing (present in *P. young*).

Foruth urosomite (Fig. 35A) with slightly larger dorsal cuticular window, but similar size and same ornamentation, consisting of only three pairs of large posterior sensilla (Nos. 41, 42 and 44); sensilla Nos. 40 and 43 missing (present in *P. young*).

Fifth urosomite (= preanal somite) (Fig. 35A) slightly narrower and longer than fourth urosomite, with largest dorsal cuticular window of all urosomites, and without any surface ornamentation; hyaline fringe well defined on all sides.

Sixth urosomite (= anal somite) (Fig. 35A, B) about 1.5 times as long as and 0.9 times as wide as preanal somite, ornamented with pair of large dorsal sensilla at base of anal operculum (No. 45), pair of large lateral cuticular pores in anterior half, and pair of ventral pores at base of caudal rami (no spinules on ventral surface), in addition to numerous shallow cuticular pits. Anal operculum well developed, unornamented on outer surface, with smooth and convex distal margin, not reaching posterior end of anal somite, representing 53% of somite's width. Anal sinus wide opened, ornamented with two long diagonal rows of slender spinules on ventral side, and one additional row on dorsal side (inner side of anal opeculum).



Fig. 35. *Parastenocaris biwae*, Male. A. habitus, dorsal view; B. anal somite and caudal rami, ventral view; C. cephalothoracic shield, lateral view (dissected); D. anal somite with spermatophore inside, ventral view; E. antennule, ventral view; F. antenna, dorsal view. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 100 μ m.

Spermatophore (Figs. 35D, 36H) about 2.3 times as long as wide, kidney-shaped, with long and narrow, curved neck.

Caudal rami (Fig. 35A, B) slender, about 3.2 times as long as greatest width (ventral view) and about 0.7 times as long as anal somite, cylindrical but tapering towards posterior end, slightly divergent, with space between them about 1.5 times of one ramus width; armed with seven elements (three lateral, one dorsal, and three apical). Ornamentation consists of large lateral cuticular pore at about 2/3 of ramus langth, and posterior ventral row of several spinules along posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at midlength, about 0.8 times as long as caudal ramus, triarticulate basally (inserted on two pseudo-joints). Lateral setae slender and smooth, inserted very close to each other also at midlenght, two larger ones more anteriorly and minute one in between and more posteriorly. Anterior lateral seta which inserted more dorsally longest, half as long as ramus, 2.3 times as long as ventral anterior seta, and about five times as long as minute (distal) seta. Inner apical seta strongest, without breaking plane, smooth, about 4.7 times as long as ramus, pointing posteriorly, with slightly curled tip inwardly. Outer apical seta also without breaking plane and smooth, relatively strong basally but much shorter, about 0.9 times as long as ramus, inserted close to dorsal surface and pointing latero-posteriorly.

Antennula (Fig. 35E) shorter than cephalothorax, slender, eight-segmented, prehensile and strongly digeniculate, ornamented with six ventral spinules on first segment distally, and with ribbed elongated chitinous plate on anterior surface of sixth segment. First segment very short, while second longest. Geniculation between third and fourth and between sixth and seventh segments; last two segments at 90° angle. Distal anterior corner of seventh segment produced into very small spiniform process, but larger proximal spiniform process present on fifth segment on anterior surface. Long aesthetasc on fifth segment reaching beyond tip of appendage for length of last segment, fused basally to slightly longer seta, relatively slender and blunt distally; much shorter and more slender apical aesthetasc on seventh segment, fused basally to two setae (acrotheck). Setal formula: 0.6.4.2.4.0.1.9. All setae slender and all, except largest seta on second segment, smooth; most setae with pore on tip; proximallmost seta on second segment unipinnate with several long spinules along anterior surface, much shorter than two large setae on fifth segment or longest apical seta on eighth segment (latter probably longest); only seta on eighth segment minute.

Antenna (Fig. 35F) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unarmed, ornamented with three short spinules. Allobasis about three times as long as wide, unarmed but ornamented with two rows of large spinules on anterior surface. Endopod 0.8 times as long as allobasis and tnearly three times as long as wide, with two parallel surface frills subdistally, ornamented with large spinules along anterior surface, armed laterally with two short spines (proximal one shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, which three times as long as segment. All antennal armature unipinnate.

Labrum large and triangular in lateral view, with narrow and straight cutting edge, without any ornamentation on anterior surface, with several parallel rows of spinules along cutting edge (those on outer distal corners strongest).

Paragnaths strongly fused into trilobite structure, with numerous distal rows of slender short spinules on lateral lobes, one distal row of minute spinules on central lobe, and another transverse row of 10 very long spinules on posterior surface of central lobe at about 2/3 of its length.

Mandibula with narrow cutting edge on elongated coxa, armed with one complex tooth ventrally,

one unipinnate seta dorsally, and several smaller teeth and/or spinules in between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on tip.

Maxillula with relatively large praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, ornamented with single spinule on posterior surface near dorsal margin, armed with lateral strong seta and four apical elements (probably three spines and one strong seta; apical spines with crown of spinules on tip, resembling small hands). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical setae (two smooth and slender, one curved and unipinnate), and single minute lateral seta. Endopod and exopod absent (fused to basis without trace), minute seta on basis probably representing remnants of exopodal armature. All coxal and basal setae, as well as smooth lateral seta on praecoxa, with pore on tip.

Maxilla composed of syncoxa, basis, and one-segmented endopod, ornamented with row of five spinules on inner side of syncoxa proximally, and with arched row of six spinules on posterior side of suncoxa close to outer margin. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with two smooth and one pinnate seta apically. Basis drawn out into strong and unipinnate claw, without seta at base, with cuticular pore on convex margin near distal tip. Endopod represented by minute segment, armed with two smooth subequal apical setae. All setae on maxilla with pore on tip.

Maxilliped with short and relatively strong syncoxa, unarmed and unornamented; basis slender, almost five times as long as wide and three times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, ornamented with several strong spinules along concave margin distally, about 0.7 times as long as basis.

First swimming leg (Fig. 36A) with unarmed praecoxa, coxa, and intercoxal sclerite. Intercoxal sclerite very small, with narrow and concave distal margin and smooth. Paecoxa ornamented with several rows of minute spinules on anterior surface. Coxa with posterior row of large spinules on posterior surface and close to outer margin. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch along distal margin at base of endopod, and several long spinules on inner margin proximally; armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin and distally on all segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin, one longer row of even longer spinules on inner margin, and three spinules on anterior surface along distal margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod, 1.2 times as long as larger geniculate exopodal seta, and almost 2.4 times as long as outer spine on endopod. All exopodal and endopodal armature unipinate along outer margin. Endopod on one leg in one male deformed (Fig. 36A), all others normal.

Second swimming leg (Fig. 36B) with smooth praecoxa and intercoxal sclerite. Intercoxal sclerite large, trapezoidal, with deeply concave distal margin. Praecoxa triangular and large. Coxa short, rhomboidal, with diagonal row of small spinules on anterior surface and two shorter rows of spinules along distal margin on posterior surface. Basis larger than coxa, semicircular, unarmed, ornamented with row of spinules on outer margin and another arched row of spinules at base of endopod. Exopod three-segmented, ornamented with large spinules along outer margin, and with distal hyaline frills



Fig. 36. *Parastenocaris biwae*. Male: A. first swimming leg with abnormal endopod (undissected); B. endopod of second swimming leg; C. third swimming leg, anterior view (undissected); D. third swimming leg, posterior view (dissected and mounted); E. tip of third leg, posterior view; F. fourth swimming leg without last two exopodal segments, posterior view; G. fifth leg, anterior view; J. second swimming leg, anterior view; K. fifth legs, anterior view. Scales: 100 μ m.

on each segment on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one 1.55 times as longer as entire exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, 5.3 times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with four large spinules along apical margin; armed apically with single smooth seta, which about 0.9 times as long as segment and pointing inwards.

Third swimming leg (Fig. 36C-E) with smooth intercoxal sclerite, which largest of all legs, trapezoidal, and with short and concave distal margin. Praecoxa not well defined on anterior surface, triangular on posterior surface, about as large as in second leg, unarmed, and unornamented. Coxa rectangular, with arched row of large spinules on anterior surface, and two row of spinules along posterior margin on posterior surface (outer minute). Basis robust, ornamented with long row of large spinules and one pore on anterior surface, armed with outer long and slender seta; distal inner corner of basis produced distally as bulbous soft semicircular lobe, partly shielding endopod. Endopod represented with single smooth and minute armature element, inserted on inner margin at 3/4 of basis length, shorter but stronger than spinules on anterior sruface. Exopod with both segments fused; ancestral proximal segment 2.5 times as long as wide, curved inwards and with thin hyaline lamelle along inner margin, and three strong and short chitinous beakes on posterior surface, ornamented with two or three minute spinules on distal outer corner; armed subapically with simple, strong, smooth and inwardly curved spine, which about as long as apophysis and more or less flat distally; ancestral distal segment (apophysis) cylindrical, oriented slightly inwards, ornamented with single pore on anterior surface; armed with single short element on top, which leaf-like, with very thin cuticulum, more or less ovoid.

Fourth swimming leg (Fig. 36F) with smooth praecoxa and intercoxal sclerite. Intercoxal sclerite shorter and smaller than in third, with equally long and concave distal margin. Praxoca small and triangular. Coxa rhomboidal, slightly larger than in second leg, unarmed, ornamented with short distal row of minute spinules on posterior surface. Basis large and more or less rectangular, armed with single smooth outer seta, ornamented with two minute spinules on outer margin at base of outer seta, and with three huge chitinous spiniform process on inner distal corner; anterior process bilobate distally and very wide; inner process spiniform and curved outward, longest; posterior process shortest but most strongly chitinized. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with strongly concave and smooth inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and long and strong apical seta; apical seta 1.2 times as long as entire exopod, and more than twice as long as outer spine. Endopod one-segmented, about as strong but longer than first exopodal segment, cylindrical proximally and bilobate distally, with inner lobus longer and stronger, ornamented with several rows of very long spinules; inner lobe smooth and with thin cuticulum.

Fifth leg (Fig. 36G) simple short cuticular plate, almost rectangular in shape, ornamented with single pore on anterior surface and single spinule at base of outermost seta, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost three times as long as entire leg; middle seta (probably ancestral outer endopodal) much shorter, 1.7 times as long as leg, and 1.4 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with small space between them, pointing caudally, not reaching distal margin of fifth pedigerous somite.

Sixth legs (Fig. 35D) smooth, unarmed and unornamented, forming simple lage operculum covering gonopore, probably both fused together or right one reduced and left one enlarged, representing 55% of somite's width.

Female: (based on single newly collected specimen). Body length, excluding caudal setae, 584 μ m. Habitus, ornamentation of prosomites, colour and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite (Fig. 37A–C) about as wide as long (ventral view), without any trace of subdivision, with oval dorsal cuticular window in anterior half, which much larger than that in male (originating from fused windows of two ancestral somites). Genital complex (Fig. 37B) occupying anterior ventral half of genital double somite; genital apertures covered by vestigial sixth legs; median copulatory pores also covered by fused sixth legs; seminal receptacles small, bell-shaped, with strongly sclerotized lateral walls; copulatory duct very short and weakly sclerotized. All posterior senislla homologous to those on male third urosomite, while all sensilla from male second urosomite missing except lateral pair (No. 33).

Third, fourth (preanal), and fifth (anal) urosomites very similar to male (Fig. 37A, B).

Caudal rami (Fig. 37A, B) slightly shorter in proportion to anal somite, about 3.7 times as long as wide in ventral (or dorsal) view, and slightly less divergent, but also cylindrical and armed and ornamented as in male.

Antennula seven-segmented, ornamented on first segment with few minute spinules on ventral surface, not geniculate, with slender aesthetasc on fourth segment, not reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, which fused basally to two apical setae; proximal aesthetasc much more slender than in male; setal formula: 0.4.5.2.1.0.9. All setae, except proximalmost one on second segment, smooth, and most setae with pore on tip.

Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 36I), and second swimming leg (Fig. 36J) same as in male.

Third swimming leg (Fig. 37C) with smooth praecoxa and intercoxal sclerite. Coxa with three large spinules on anterior surface, and two rows of spinules along distal margin on posterior surface, unarmed. Basis ornamented with several large spinules on outer margin distally and another row of smaller spinules at base of endopod, armed with very long and smooth outer seta, which 0.8 times as long as entire exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate; apical seta 1.5 times as long as entire exopod. Endopod one-segmented, small, cylindrical and unornamented, armed with apical spiniform bipinnate element on tip, which basally fused to segment, reaching 4/5 of first exopodal segment in length.

Fourth swimming leg (Fig. 37D) without spiniform processes on basis. Endopod one-segmented, slender and long, cylindrical, curved inwards, ornamented with apical row of five large spinules at base of apical spine (no lateral spinules on inner margin); apical spine not distinct at base, bipinnate and robust, and about 0.7 times as long as endopod; endopod with apical spine almost reaching posterior margin of third exopodal segment in length. Exopod similar to male, but inner margin of first exopodal segment not as much concave; apical seta nearly 1.2 times as long as entire exopod.

Fifth leg (Figs. 36K, 37B) also simple cuticular plate, but with inner distal corner produced into strong and blunt spiniform process, which about 1.4 times as long as rest of leg, reaching in length tips of innermost seta; armature and ornamentation same as in male, except spinule at base of outermost seta (or very reduced setae) somewhat longer.

Sixth legs vestigial (Fig. 37B), narrowly fused into simple cuticular flap, covering gonopore, unornamented and unarmed; distal margin thin, medial part very short, lateral part longer and bilobate, each lobe terminating into more or less sharp tip.


Fig. 37. *Parastenocaris biwae*, Female. A. urosome, lateral view; B. urosome, ventral view; C. third swimming leg, anterior view; D. fourth swimming leg, anterior view. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 100 μ m.

TYPE LOCALITY: Japan, Shiga Prefecture, Lake Biwa, western shore, Shirahige, sandy beach.

DISTRIBUTION: This species is only known from the Lake Biwa drainage area in Japan, but it is a rare species there these days. Our repeated efforts to collect this species from the lake's shore (including the type locality) failed despite more than 30 samples taken in 2009 and 2010. As a part of the survey of subterranean biodiversity in the Lake Biwa drainage are, more than 100 samples were taken from 2008 to 2011, from caves, wells, river and lake interstitial, and the species was found in only one sample represented by three individuals.

ECOLOGY: Specimens were obtained from the interstitial on the river banks, but the type locality is interstitial of a beach on the Lake Biwa shore. Relatively large size of this species suggests that it prefers gravelly rather than sandy sediments. The confluence of Daido and Seta rivers is a mixture of medium size sand, gravel and large rocks.

SPECIMEN EXAMINED: Two males (NIBRIV0000232643 and NIBRIV0000232644) and one female (NIBRIV0000232645), each dissected on one slide; Japan, Shiga Prefecture, Lake Biwa drainage area, confluence of Seto and Daido rivers, sandy/gravely beach, 27 September 2009, leg. T. Karanovic.

REMARKS: Reid (1995) examined some specimens of this species and synonymized it with the widely distributed *P. brevipes*, although she noted that "… specimens from Lake Biwa, Japan, presented a series of consistent differences from most other populations examined" (Note: other populations examined were either from northern Europe or North America). She especially pointed out the reduced and spiniform endopod of the third leg in male (as opposed to a slender and long seta in non-Asian populations). Chang (2009, 2010) reported *P. brevipes* for the first time from Korea, providing a limited set of drawings. Karanovic and Lee (2012) examined both Korean and Japanese populations, and showed them to be distinct species (although closely related), differing in a number of morphological characters. Three possible hypotheses emerged: either they were dealing with three different species, or one of the Asian populations is conspecific with *P. brevipes*. As both Korean and Japanese specimens have the same shape and size of the third leg endopod in male, it is most probable that they shared an immediate common ancestor, i.e. we are dealing with three different species. Thus Karanovic and Lee (2012) reinstated *P. biwae* as a valid species, and described the Korean population as a new species. Major differences between the Japanese and Korean species were listed in the remarks section for the latter (see below).

27. Parastenocaris brevipes Kessler, 1913 (Figs. 38, 39)

Parastenocaris brevipes Kessler, 1913a, p. 514, figs. 1–9; Kessler, 1913b, p. 250, figs. 1–6; Pesta, 1932, p. 155, fig. 87; Lang, 1948, p. 1223, fig. 491-1; Borutzky, 1952, p. 398, figs. 109/1–12, 111; Chappuis, 1958, p. 431, fig. 16; Monchenko, 1964, p. 545, figs. 1, 2; Dussart, 1967, p. 410, fig. 178; Enckell, 1969, p. 500; Dussart and Defaye, 1990, p. 226; Reid, 1995, p. 174, figs. 1–4 (except fig. 2i).

Parastenocaris starretti Pennak, 1939, p. 224, figs. 1–10; Borutzky, 1952, p. 408; Chappuis, 1958, p. 431, fig. 15; Dussart and Defaye, 1990, p. 236.

Parastenocaris wilsoni Borutzky, 1952, p. 400.

[non] Parastenocaris biwae Miura, 1969, p. 40, figs. 1-15; Dussart and Defaye, 1990, p. 254.

[non] Parastenocaris brevipes Kessler: Reid, 1995, p. 177, fig. 2i; Lee and Chang, 2009, p. 176, fig. 6; Chang, 2009, p. 225, fig. 96; Chang, 2010, p. 91, fig. 41.

Note: for a full list of synonyms see Lang (1948) and Reid (1995).

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 324 to 516 μ m). Preserved specimen white. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus cylindrical and very slender, without demarcation between prosome and urosome; greatest width difficult to establish. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, without surface ornamentation except sensilla and pores (no spinules) and in some specimens shallow cuticular pits, dorsally with round cuticular double window on cephalothorax and simple oval cuticular windows on genital and three postgenital somites (Fig. 38A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax about 1.5 times as long as wide in dorsal view; representing about 20% of total body length. Ornamentation of surface of cephalic shield with sensilla relatively simple, with eight sensilla surrounding dorsal cuticular window. Free somites with eight sensilla in total, except preanal somite, which lacks any ornamentation, and anal somite.

Anal somite (Fig. 38A) much longer than preanal somite, ornamented with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with slightly concave and smooth distal margin, not reaching posterior end of anal somite, representing 70% of somite width. Anal sinus widely opened, ornamented with multiple rows of fine spinules.

Caudal rami (Fig. 38A, B) about 3.5 times as long as greatest width (dorsal view) and only 0.7 times as long as anal somite, cylindrical but slightly tapering towards distal end, slightly divergent, with space between them about 1.5 times one ramus width, unornamented; armed with seven armature elements (three lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at midlength, about 0.6 times as long as caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other, also at midlength. Proximalmost lateral seta placed more dorsally, 0.6 times as long as ramus, about four times and long as middle seta (minute), about twice as long as distalmost (ventralmost) one. Inner apical seta short and smooth, inserted more ventrally, about 0.7 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about five times as long as outer apical seta or caudal ramus. Outer apical seta also without breaking plane and smooth, relatively strong basally but much shorter, about as long as ramus.

Antennula (Fig. 38C) relatively long, seven-segmented, prehensile and strongly digeniculate, ornamented with few spinules on first segment. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as small spiniform process; another small spiniform process present on fourth segment basally. Slender aesthetasc on fourth segment reaching beyond tip of appendage, fused basally to equally long seta. Somewhat shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula: 0.5.4.4.0.0.8. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 38D) relatively slender and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, ornamented with few spinules, unarmed.



Fig. 38. *Parastenocaris brevipes*, Male. A. urosome, dorsal view; B. anal somite and caudal rami, ventral view; C. antennula; D. antenna; E. mandibula; F. maxilla; G. maxilliped; H. first swimming leg, anterior view; I. second swimming leg, anterior view; J. third swimming leg, anterior view; K. fourth swimming leg, anterior view; L. fifth leg, anterior view. Scales: 50 μ m (cited from Reid, 1995, modified).

Allobasis about three times as long as wide, unarmed, and ornamented with short row of large spinules on anterior surface. Endopod about 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two spines and apically with five strong armature elements (two of which are geniculate), all of them unipinnate. Exopod minute, cylindrical, about three times as long as wide, unornamented, armed with only apical seta, about 2.3 times as long as segment.

Mandibula (Fig. 38E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula with relatively small praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 38F) ornamented with single spinule basally on inner margin, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal endite armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong and pinnate claw, probably without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 38G) with short and relatively strong syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and as many times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, ornamented with several spinules along concave margin distally, about 0.8 times as long as basis.

First swimming leg (Fig. 38H) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with row of small spinules on distal margin, additional row of larger spinules on outer margin, but unarmed. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two several rows of large spinules on outer margin and one row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.4 times as long as entire endopod and longer than longest seta on exopodal.

Second swimming leg (Fig. 38I) with smooth praecoxa, and intercoxal sclerite. Coxa ornamented with few spinules on anterior surface, unarmed. Basis unarmed, ornamented with row of large spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost longest; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and elongated, about five times as long as wide, reaching 1/4 of first exopodal segment in length, ornamented with several large spinules along apical margin; armed apically with one smooth seta, about as long as segment and points inwards.

Third swimming leg (Fig. 38J) with smooth praecoxa, coxa, and intercoxal sclerite, (coxa sometimes

with two or three spinules on anterior surface). Basis relatively small, shorter than coxa, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin, and longitudinal row of small spinules along inner margin. Endopod represented by slender seta, slightly larger than largest spinules on basis. Exopod with both segments fused; ancestral proximal segment 2.5 times as long as wide, curved inwards and slowly tapering towards distal end, with small chitinous beak on inner margin proximally, ornamented with few short spinules on outer margin distally, armed subapically with simple, smooth and curved spine, about as long as apophysis; ancestral distal segment (apophysis) spiniform, oriented inwards, unornamented, simple structure, ending in ball-like structure; exopodal spine and apophysis almost parallel.

Fourth swimming leg (Fig. 38K) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into two processes; inner process bifurcate, ending in two sharp spiniform tips and less strongly sclerotised, smooth and nearly parallel to endopod (although tips pointing slightly outwards); outer process much broader and longer, more strongly sclerotised, bicuspidate, pointing distally, complex tridimensional structure, partly shielding proximal part of endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave and smooth inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and much longer apical seta; apical seta about 0.9 times as long as entire exopod and almost twice as long as outer spine. Endopod one-segmented, complex tridimensional structure, bilobate distally and armed with two rows of large spinules in cleft, unarmed, somewhat longer than first exopodal segment.

Fifth leg (Fig. 38L) simple small trapezoidal cuticular plate, with inner distal corner not produced, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, almost 3.2 times as long as entire leg; next seta (probably ancestral exopodal) very small and probably fused basally, almost looks like spinule; third seta from outer side (ancestral outer endopodal) 1.7 times as long as leg, and 1.5 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, or sometimes fused to each other with very narrow bridge.

Sixth legs smooth, unarmed and unornamented, forming trapezoidal flap.

Female: Body length, excluding caudal setae, from 360 to 497 μ m. Habitus (Fig. 39A), ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double (Fig. 39A) somite about as long as wide (dorsal view), without trace of subdivision, with large saddle-like dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male, but dorsal cuticular windows slightly larger and anal somite somewhat shorter in proportion to preanal somite.

Caudal rami (Fig. 39A) similar to male but slightly larger in proportion to anal somite; armature similar to male, but outer apical seta proportionately shorter.

Antennula (Fig. 39B) also seven-segmented but not prehensile, ornamented with spinules only on first segment, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and somewhat shorter apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula: 0.4.6.3.1.0.9. All setae smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 39C), second swimm-

ing leg (Fig. 39D), and exopod of fourth swimming leg (Fig. 39F) similar to male.

Third swimming leg (Fig. 39E) with large praecoxa, smooth coxa and intercoxal sclerite. Basis smaller, ornamented with several large spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, spiniform, straight, unornamented, armed with apical strong spine fused basally to segment, not reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 39F) without spiniform processes on basis, but with row of small spinules at base of endopod. Endopod one-segmented, very long and slender, ornamented with transverse apical row of spinules at base of apical spine, fused at base, bipinnate, straight, and about as long as endopod; endopod with apical spine reaching 2/3 of third exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 39G, H) also simple cuticular plate, but with inner distal corner produced into longer spiniform process. Armature and ornamentation same as in male. Length of inner process varies among different populations.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed.

TYPE: Type material probably lost (Reid, 1995).

TYPE LOCALITY: Germany, Saxony, Bautzen district, Schwepnitz village, Sphagnum bog.

DISTRIBUTION: This species seems to have a wide Holarctic distribution, being recorded in northern Europe and North America. Reid (1995) considered this species also present in Asia, as she synonymized the Japanese *P. biwae* with it, but Karanovic and Lee (2012) argued that *P. biwae* is a distinct species. Chang (2009, 2010) reported *P. brevipes* from Korea, but Karanovic and Lee (2012) describe the Korean population as a new species. This leaves no confirmed records of this species in Asia.

ECOLOGY: This is one of a few parastenocaridids recorded from surface-water habitats. Borutzky (1952) even speculated that its distribution mirrors that of *Sphagnum* bogs, although it is not clear where exactly it lives in this habitat. Other than *Sphagnum* bogs, the species has been recorded from numerous interstitial and subterranean habitats. It is especially common in interstitial habitats in lake beaches.

REMARKS: This species was redescribed by Reid (1995), who examined a wide range of samples from Europe, North America, and Japan. She synonymized several taxa (see the synonymy section above) for the first time, including the Japanese *P. biwae. Parastenocaris brevipes* is unique among parastenocaridid copepods in its very wide Holarctic distribution. Reid (1995) argued that this broad longitudinal distribution could be explained by the fact that *P. brevipes* often attains high populations in bogs, where it may be easily transported by aquatic birds and mammals. In that case, populations in southern latitudes in interstitial habitats would represent glacial relicts. Unfortunately, this was never tested with molecular methods. Chang (2009, 2010) reported *P. brevipes* from Korea, but Karanovic and Lee (2012) noted some unusually high variability among three disjunct populations in South Korea, which could be indicative of species- or subspecies-level diferences, and also a number of differences from the Japanese population. As it became clear that the Japanese and Korean populations do not belong to the same species, they argued for the reinstatement on the Japanese *P. biwae* and described the Korean populations as a new species (see above and below). However, it is possible that even this narrowly defined *P. brevipes* (distributed in Europe and North America) will prove to be a species complex, rather than one widely distributed species, as indicated by various lengths of



Fig. 39. *Parastenocaris brevipes*, Female. A. urosome, dorsal view; B. antennula; C. first swimming leg, anterior view; D. second swimming leg, anterior view; E. third swimming leg, anterior view; F. fourth swimming leg, anterior view; G. fifth leg, anterior view; H. fifth leg of another specimen, anterior view. Scales: 50 μ m (cited from Reid, 1995, modified).

the inner distal process on the female fifth leg (Fig. 39G, H) reported by Reid (1995). We have to point out that Reid (1995) did not examine fine ornamentation of somites or appendages, nor did she provide any SEM photographs of various populations, and in the light of the recently discovered short range endemism in this family (Karanovic and Cooper 2011a; Karanovic et al., 2012) such treatment is unlikely to reveal closely related allopatric species in this very conservative group of copepods.

28. Parastenocaris brincki Enckell, 1970 (Fig. 40)

Parastenocaris brincki Enckell, 1970, p. 551, figs. 27-30.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 360 μ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of anal somite and caudal rami (Fig. 40A), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented only with sensilla and pores (no cuticular pits or spinules). Presumably preanal somite and three anterior somites with large, oval dorsal cuticular windows, just as in *P. irenae* Enckell, 1970 (see above). Anal somite (Fig. 40A) ornamented only with pair of dorsal sensilla at base of anal operculum. Anal operculum (Fig. 64A) well developed, unornamented on outer surface, with straight caudal margin, reaching posterior end of anal somite. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 40A) about 3.2 times as long as greatest width (lateral view) and almost 0.9 times as long as anal somite, cylindrical, armed with six armature elements (two lateral, one dorsal, and three apical), ornamented with single spinule on distal margin ventrally. Dorsal seta slender and smooth, inserted at 3/5 of ramus length and somewhat closer to inner margin, about 0.7 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other, also at 3/5 of ramus length. Proximal lateral seta inserted more dorsally, about 4.5 times as long as distal minute one, and about 0.4 times as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, half as long as ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta much smaller than middle apical seta and not very strong, also without breaking plane, smooth, about 0.7 times as long as ramus.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown, but presumably similar to those in type species.

Second swimming leg composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod; similar in shape, armature, and ornamentation to that of *P. irenae* and *P. noodti* Enckell, 1970 (see above).

Third swimming leg (Fig. 40B, C) with coxa and basis fused, forming a robust coxobasis ornamented with distal row of five long spinules close to outer margin. Endopod very small, one-segmented, hardly larger than basal spinules, pointing inwards. Exopod with both segments fused; ancestral proximal segment about twice as long as wide, with straight inner margin and large chitinous beak on outer margin, ornamented with two or three large spinules on outer margin distally, armed subapically with short, smooth and curved spine, half as long as apophysis; ancestral distal segment (apophysis) cylindrical, oriented inward, unornamented but with minute spiniform process apically, fused to segment; complex tridimensional structure of apophysis ends with membraneous leaf-like part.

Fourth swimming leg (Fig. 40D) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process slightly longer but less strongly sclerotised, smooth and sharply pointed, pointing inwards; outer process somewhat smaller, but more strongly sclerotised, pointing outward, reaching outer margin of endopod, and shielding proximal part of endopod. Basis ornamented with transverse row of large spinules on anterior surface, closer to inner margin. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, three times as long as greatest width, with stout outer distal spine, almost 0.9 times as long as segment. Endopod one-segmented, very inflated basally from anterior view, slightly shorter than first exopodal



Fig. 40. *Parastenocaris brincki*, Male. A. anal somite and left caudal ramus, lateral view; B. third leg; C. distal part of third leg, different view; D. basis, endopod, and first exopodal segment of fourth leg; E. fifth leg. Scales: 50 μ m (cited from Enckell, 1970, modified).

segment, and almost parallel with it, armed with single smooth seta apically (broadly fused basally to segment), ornamented with single spinule subdistally and with a diagonal row of thin spinules (or striae?) on anterior surface. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 68E) simple trapezoidal cuticular plate, inner distal margin produced posteriorly into long smooth spiniform process, without ornamentation, armed with two endopodal smooth setae; basal seta probably broken off during dissection; outer endopodal seta slightly longer than inner one.

Sixth legs unknown, probably very similar to type species. **Female**: unknown.

Туре: Type material lost.

TYPE LOCALITY: Sri Lanka, Sabaragamuwa Province, Bopathella Falls, 14.5 km east of Ratnapura, interstitial in a sandy bank below the fall and surrounded by water.

DISTRIBUTION: Known only from the type locality, Bopathella Falls near Ratnapura, Sabaragamuwa Province, Sri Lanka.

ECOLOGY: This is also an interstitial species. Only one male was collected at the type locality, so it is possible that the prime habitat for this species was not sampled. Interestingly, *P. brincki* lives together with three other parastenocaridids, all of which are relatively closely related and certainly belong to the *brevipes* group. Therefore, it is reasonable to expect some habitat partitioning, and perhaps the prime habitat of this species lies in the deeper sediment that could not be reached effectively with the sampling method employed.

REMARKS: Although the original description of this species by Enckell (1970) is incomplete, the shape of the fourth leg basis and endopod would suggest it belongs to the *brevipes* group of Lang (1948). Enckell (1970) recognised this, but did not comment on the affinities of his new species, although the description seems to be comparative to that of two below-presented species: *P. irenae* and *P. noodti* (see below). *Parastenocaris brincki* shares with *P. irenae* the same produced inner distal corner of the male fifth leg (Fig. 40E), unlike any other Sri Lankan species from this group. The former, however, can be distinguished from the latter by longer anal somite and caudal rami, much shorter outer apical caudal seta, and a strong, pointed outer process on the first exopodal segment of the male third leg. The shape of the male fourth leg endopod and basal processes (that together form a complex structure, see Fig. 40D) cannot be found in any other species of the genus. Parasteno-caris brincki seems to be also the only Sri Lankan species with a row of large spinules on the basis of the male fourth leg (Fig. 40D).

29. Parastenocaris feuerborni Chappuis, 1931 (Fig. 41)

Parastenocaris feuerborni Chappuis, 1931, p. 513, figs. 130–141; Lang, 1948, p. 1231, fig. 495-7; Chappuis, 1958, p. 431, fig. 17.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), about 300 μ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of anal somite and caudal rami of female (Fig. 41A), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites probably smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument probably weakly sclerotised as in other closely related species, smooth, without surface ornamentation except sensilla and pores (no spinules or cuticular pits). No cuticular windows on cephalothorax or urosomal somite. Anal somite 1.4 times as long as wide, probably with pair of large dorsal sensilla at base of anal operculum (although these reported as absent in original description). Anal operculum well developed, unornamented on outer surface, with concave caudal margin, almost reaching posterior end of anal somite, and representing 62% of somite width. Anal sinus widely opened, without ornamentation.

Caudal rami about three times as long as greatest width (dorsal view), much shorter than anal somite, conical (slowly narrowing towards distal end), slightly divergent, with space between them 1.5 times one ramus width, armed with six armature elements (two lateral, one dorsal, and three apical), unornamented. Dorsal seta slender and smooth, inserted slightly posteriorly to midlength, somewhat closer to inner margin, about half as long as caudal ramus, probably triarticulate basally.

Lateral setae thin and smooth, inserted close to each other, at 3/5 of ramus length. Proximal lateral seta inserted more dorsally, about twice as long as distal minute one, and about 0.35 times as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, half as long as ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta smaller than middle apical seta but also strong, also without breaking plane, smooth, about 0.7 times as long as ramus.

Rostrum, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown, but presumably similar to those in type species.

Antennula (Fig. 41B) relatively long, seven-segmented, prehensile and strongly digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as large and sharp spiniform process; another smaller spiniform process present on fourth segment basally. Armature unknown.

First swimming leg with first endopodal segment slightly longer than first two exopodal segments combined.

Second swimming leg (Fig. 41C) composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and three elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. Endopod cylindrical and relatively short, about 2.6 times as long as wide, reaching middle of first exopodal segment in length, ornamented with four large spinules along distal margin; armed apically with one smooth, slender inwards-pointing seta, about as long as segment.

Third swimming leg (Fig. 41D, E) with smooth praecoxa and coxa. Basis robust, trapezoidal, armed with smooth outer seta, ornamented with 11 long spinules on outer margin. Endopod very small segment, unornamented, armed with single apical element. Exopod with both segments fused; ancestral proximal segment about 3.3 times as long as wide, with chitinous serrate structure on distal part of inner margin, unornamented, armed subapically with simple, smooth, and very small spine, 0.7 times as long as apophysis; ancestral distal segment (apophysis) much wider proximally, oriented inward, unornamented and unarmed, simple spiniform, smooth structure.

Fourth swimming leg (Fig. 41F, G) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process smaller, smooth and curved, simple spiniform structure, parallel to inner margin of endopod; outer process slightly larger and complex, pointing outward, and shielding proximal part of endopod. Exopodal armature and ornamentation presumably similar to that in , i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with inner margin concave proximally and convex distally, three times as long as greatest width, with stout outer distal spine, 0.8 times as long as segment. Endopod one-segmented, inflated, about 0.8 times as long as first exopodal segment, pointing distally, unarmed, ornamented with three large spinules close to distal margin. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 41H) simple rectangular cuticular plate, inner distal margin not produced posteriorly, ornamented with one spinule (or perhaps minute seta?) next to basal seta and one spinule on inner margin distally, armed with three smooth setae; outermost seta (ancestral basal one) longest, 2.5 times as long as entire leg, twice as long as middle seta, and about 3.8 times as long as inner seta (middle



Fig. 41. *Parastenocaris feuerborni*. Female: A. anal somite and right caudal ramus, dorsal view. Male: B. antennula, without armature; C. basis, endopod and first exopodal segment of second swimming leg; D. third swimming leg, lateral view; E. third swimming leg, anterior view; F. basis, endopod, and first exopodal segment of fourth swimming leg, posterior view; G. basis, endopod, and first exopodal segment of fourth swimming leg, anterior view; H. fifth legs. Female: I. endopod of second swimming leg; J. endopod of third swimming leg; K. endopod of fourth swimming leg; L. fifth leg. Scales: unknown (cited from Lang, 1948, modified).

and inner setae probably of endopodal origin).

Sixth legs unknown, probably very similar to type species.

Female: Body length significantly larger than in male, about 350 μ m. Habitus, and presumably also ornamentation of somites, colour, and nauplius eye, similar to male.

Genital double somite unknown. Anal somite and caudal rami (Fig. 41A) same as in male, but anal operculum somewhat strongly developed. Antennula unknown, probably similar to type species. Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg probably similar to male.

Second swimming leg (Fig. 41I) also similar to male, but first exopodal segment with inner margin not concave, and proportionately larger endopod.

Third swimming leg (Fig. 41J) composed of praecoxa, coxa, intercoxal sclerite, basis, two-segmented exopod, and one-segmented endopod. Endopod small and simple, fused basally to apical bipinnate spine.

Fourth swimming leg (Fig. 41KI) without spiniform processes on basis. Endopod one-segmented, slender, curved slightly inwards, ornamented with transverse apical row of two spinules at base of apical spine, distinct at base, bipinnate, and about 1.4 times as long as endopod. Exopod similar to male, except first segment with straight inner margin.

Fifth leg (Fig. 41L) much longer than in male, with large inner distal spiniform process, and no ornamentation on inner margin; all setae also proportionately shorter than in male, but armature basically same.

Sixth legs unknown but probably vestigial, fused into simple cuticular plate, covering gonopore; ornamentation and armature unknown.

TYPE: Type material lost.

TYPE LOCALITY: Indonesia, Sumatra, Lake Singkarak, washings from foliage on the shores of the lake.

DISTRIBUTION: The species is known only from the type locality, Lake Singkarak in Sumatra, Indonesia.

ECOLOGY: This species was collected from forest foliage washings on the lake shore, which makes it possible that it is not an obligate stygobiont. Of course, we do not know if the species lives in any other habitats in that lake. However, this is one of only a few species from the family Parasteno-carididae Chappuis, 1940 that was collected from outside the proper subterranean realm.

REMARKS: A remarkable size difference between male and female, as well as the armature and ornamentation of the fifth leg and proportions of the second leg endopod, would suggest a possibility that they belong to two different species, i.e., that more than one species of *Parastenocaris* lives in leaf litter on the shores of Lake Singkarak in Sumatra.

30. Parastenocaris gayatri Ranga Reddy, 2001 (Fig. 42)

Parastenocaris gayatri Ranga Reddy, 2001, p. 708, figs. 1-4.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 420 to 520 μ m (470 μ m in holotype). Preserved specimen colourless. Nauplius

eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 42A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width difficult to establish. Body length/width ratio about 9.5; cephalothorax as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, without surface ornamentation except sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites (Fig. 42A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla (sometimes joined, producing the illusion of an apical spinule), linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax (Fig. 42A) about 1.7 times as long as wide in dorsal view; representing 19 % of total body length. Ornamentation of surface of cephalic shield with sensilla unknown, as well as those of other somites.

Anal somite (Fig. 42B) probably ornamented with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 68% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 42A, B) about three times as long as greatest width (dorsal view) and almost 0.6 times as long as anal somite, cylindrical (slightly narrowing towards distal end), slightly divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large spinule ventrolaterally close to posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/5 of ramus length, about 0.6 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other also at 3/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.4 times as long as ramus, about 2.8 times and long as middle seta, and 5.2 times as long as distalmost (ventralmost) minute seta. Inner apical seta small, smooth, inserted more ventrally, about as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 3.2 times as long as outer apical seta and almost 0.3 times as long as whole body. Outer apical seta also without breaking plane and smooth, relatively strong basally, about 1.3 times as long as ramus.

Antennula (Fig. 42C) relatively long, seven-segmented, prehensile and strongly digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as large and sharp spiniform process; another large spiniform process present on fourth segment basally, furnished with small spine (or large spinule?). Slender aesthetasc on fourth segment reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to at least one seta. Setal formula (probably incomplete): 0.5.2.2.0.0.7. All setae slender and all except largest seta on second segment smooth.

Antenna (Fig. 42D) relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 3.7 times as long as wide, unarmed, ornamented with two short rows of minute spinules on anterior surface. Endopod

about 0.6 times as long as allobasis and 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about 2.3 times as long as wide, unornamented but armed with single unipinnate apical seta, twice as long as segment.

Mandibula (Fig. 42E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between them. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 42F) with relatively small praecoxa, arthrite rectangular, about 1.4 times as long as wide in lateral view, unornamented but armed with strong lateral seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two smooth apical setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 42G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, each armed apically with two smooth setae, dorsal endite much longer. Basis drawn out into strong and smooth claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 42H) with very short syncoxa, unarmed and unornamented; basis slender, about 5.3 times as long as wide and almost ten times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.7 times as long as basis.

First swimming leg (Fig. 42I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of small spinules on inner margin, armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.3 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 42J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with one outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.5 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about 6.9 times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along apical margin; armed apically with one smooth short seta, about 0.3 times as long as segment and pointing inwards.

Third swimming leg (Fig. 42K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with one long spinule and diagonal row of small spinules close to outer margin. Endopod a minute but distinct segment, about as long as largest spinule on outer margin and only slightly stronger, unornamented and armed apically with smooth seta basally

fused to segment. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and gently tapering towards distal end, with three chitinous beaks on inner margin, two distal ones especially well developed, ornamented with short row of spinules on outer distal margin, armed subapically with simple, strong, smooth and curved spine, somewhat shorter than apophysis; ancestral distal segment (apophysis) conical, oriented inwards, unornamented, with chitinous beak on inner margin distally, armed with single strong and smooth spine on top, about as long as spine on first exopodal segment.

Fourth swimming leg (Fig. 42L, M) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into two processes; inner process very narrow and less strongly sclerotised, smooth and nearly parallel to endopod; outer process much broader and more strongly sclerotised, pointing outward but then apical tip turned inwards, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 0.9 times as long as entire exopod and 2.5 times as long as outer spine. Endopod one-segmented but somewhat constricted at 2/3, slightly longer than first exopodal segment, with beak-like structure on top (probably formed by fused apical spine and spinule), parallel to exopod, additionally ornamented with diagonal row of shorter or longer spinules at distal part.

Fifth leg (Fig. 42N) simple semicircular cuticular plate, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, 3.5 times as long as entire leg; next seta (probably ancestral exopodal) very small and spiniform, almost resembling a spinule; third seta from outer side (ancestral outer endopodal) 0.8 times as long as leg, and 0.6 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 430 to 500 μ m (500 μ m in allotype). Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite slightly longer than wide (ventral view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male, but anal somite ornamented with spinules dorsolaterally (Fig. 42O).

Caudal rami (Fig. 42O) similar to male but slightly shorter in proportion to anal somite and additionally ornamented with spinules both on outer margin anteriorly and on inner margin anteriorly and posteriorly; armature same as in male.

Antennula (Fig. 42P) also seven-segmented, unornamented, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (possibly not complete): 0.4.4.2.1.0.8. All setae, except proximalmost one on second segment, smooth. Length ratio of antennular segments, from proximal end, 1:2.8:1.6:1:0.6:0.9:1.5.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg similar to male.



Fig. 42. *Parastenocaris gayatri*. Male: A. habitus, dorsal view; B. anal somite and caudal rami, dorsal view; C. antennula; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. fourth swimming leg; M. distal part of endopod of fourth swimming leg, different view; N. fifth leg. Female: O. posterior part of anal somite and left caudal ramus, dorsal view; P. distalmost five segments of antennula; Q. third swimming leg; R. coxa, basis, endopod, and first exopodal segment of fourth swimming leg; S. fifth leg. Scales: 50 μ m (cited from Ranga Reddy, 2001, modified).

Third swimming leg (Fig. 42Q) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with three spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and strong apical seta; all elements bipinnate. Endopod one-segmented, small, straight, unornamented, armed with strong apical spine, fused basally to segment, not reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 42R) without spiniform processes on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, curved outwards, and about as long as endopod; endopod with apical spine reaching middle of second exopodal segment in length. Exopod similar to male, but with inner margin less concave.

Fifth leg (Fig. 42S) also simple cuticular plate, but with inner distal corner produced into long and spiniform process. Armature and ornamentation same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed.

TYPE: Type material in the Natural History Museum in London.

TYPE LOCALITY: India, Andhra Pradesh, River Krishna at Vijayawada, near bridge at Kanaka Durga Varadhi, interstitial 10 m from water edge and at a depth of 10 to 30 cm, fine sands.

DISTRIBUTION: This species is only known from the type locality, River Krishna at Vijayawada, India.

ECOLOGY: It was collected from fine sands on a river bank, about 10 m from the water's edge, at a depth of about 10 to 30 cm. It lives in the same habitat as two other parastenocaridids, *P. sandhya* Ranga Reddy, 2001 and *P. savita* Ranga Reddy, 2001, but it seems to be separated temporally. In particular, the other two species were collected there in August, while *P. gayatri* was collected in February (see above).

REMARKS: Presence of dorsal cuticular windows on anal somites and shape of the fourth leg basis and endopod clearly place this species in the *brevipes* group of Lang (1948). In the original description, Ranga Reddy (2001) remarked that *P. gayatri* is probably most closely related to *P. savita*, but can be distinguished by the ornamentation of the caudal rami and fifth leg in female, shape of the second-leg endopod and fifth leg in female, and especially by the shape and ornamentation of the third and fourth legs in male. Dorsal cuticular windows are also more pronounced in *P. gayatri*, and there is an additional window on the genital somite in male, and a larger one (derived from the fusion of two ancestral windows) in female. The third species that lives in the same habitat with these two congeners (*P. sandhya*) is only remotely related.

31. Parastenocaris hinumaensis Kikuchi, 1970 (Fig. 43)

Parastenocaris hinumaensis Kikuchi, 1970, p. 170, figs. 1, 2.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 349 μ m. Preserved specimen colourless. Nauplius eye absent. Body cylindrical, vermiform, composed of prosome (consisting of cephalothorax and three free pedigerous somites, the first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Hyaline

fringes of somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented with sensilla and pores at least on some somites (no cuticular pits or spinules). Information on cuticular windows not available. Anal somite (Fig. 43A) probably ornamented only with pair of dorsal sensilla at base of anal operculum. Anal operculum well developed, with slightly convex caudal margin, unornamented on outer surface but with row of very slender spinules on distal margin (probably on ventral surface), not reaching posterior end of anal somite. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 43A) about 3.3 times as long as greatest width (ventral view), cylindrical in anterior part but conical in posterior part, divergent, with space between them about 1.5 times one ramus width, armed with at least four armature elements (one lateral, one dorsal, and two apical), unornamented. Dorsal seta slender and smooth, inserted at 3/5 of ramus length and much closer to its inner margin, about 0.8 times as long as caudal ramus, probably triarticulate basally. Lateral seta thin and smooth, inserted also at 3/5 of ramus length and more ventrally, about 0.4 times as long as ramus. Inner apical seta probably reduced or very small and not observed. Principal apical seta strongest, without breaking plane, length unknown. Outer apical seta smaller than principal apical seta but also relatively strong, also without breaking plane, smooth, length unknown.

Ornamentation of somites, rostrum, labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped unknown, but presumably similar to those in type species.

Antennula (Fig. 43B) long, seven-segmented but first segment not illustrated, prehensile and strongly digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of fourth segment protrudes as small spiniform processes; another spiniform process present on sixth segment, together making powerful pincers. Slender aesthetasc on fourth segment not illustrated, probably fused basally to slightly longer seta. Much shorter apical aesthetasc on eighth segment also not illustrated, probably fused basally to two setae. Setal formula (probably incomplete): 0.5.1.1.2.0.5. All setae slender and smooth. Largest seta on second segment most proximally.

Antenna and first swimming leg similar to that in female (see below).

Second swimming leg (Fig. 43C) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Exopod ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about as long as exopod; all exopodal armature bipinnate. Endopod cylindrical and relatively slender, about 3.8 times as long as wide, reaching middle of first exopodal segment in length, ornamented with three large spinules along distal margin; armed apically with one smooth, slender, inwards-pointing seta, about as long as segment.

Third swimming leg (Fig. 43D) with praecoxa and coxa unornamented and relatively small. Basis robust, rhomboidal, armed with large outer smooth seta, ornamented with nine long spinules on anterior surface diagonally from base of outer seta to distal inner corner, and longitudinal row of small spinules along inner margin. Endopod absent. Exopod with both segments fused; ancestral proximal segment about 3.7 times as long as wide, cylindrical in proximal part and conical in distal half, with slightly convex inner margin, with small cuticular protrusion on anterior surface at middle, unornamented, armed subapically with simple, strong, smooth and curved spine, 0.8 times as long as apophysis; ancestral distal segment (apophysis) conical, oriented inwards, unornamented but with minute spiniform process apically, basally fused to segment.

Fourth swimming leg (Fig. 43E) composed of praecoxa, coxa, intercoxal sclerite, basis, three-

segmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process slightly longer but less strongly sclerotised, linguiform, smooth and parallel to endopod; outer process somewhat shorter but much broader and more strongly sclerotised, bilobate, pointing outward, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, curved, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with almost straight inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and long and strong apical seta; apical seta 0.9 times as long as entire exopod and 2.5 times as long as outer spine. Endopod one-segmented, curved inwards, with inflated inner margin distally, slightly longer than first exopodal segment, ornamented with single large spinule on outer margin at 3.5 of its length. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 43F) simple rectangular cuticular plate, inner distal margin unornamented and not produced posteriorly, unornamented, armed with four smooth setae; outermost (ancestral basal) seta 3.6 times as long as next seta (probably ancestral exopodal), as well as innermost one, and 7.2 times as long as innermost seta (two inner setae probably ancestral endopodal armature).

Sixth legs unknown, probably very similar to type species.

Female: Body length, excluding caudal setae, 374 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite (Fig. 43G).

Genital double somite (Fig. 43G) about as long as wide without trace of subdivision; ornamentation unknown; genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male. Anal operculum (Fig. 43H) with almost straight caudal margin.

Caudal rami (Fig. 43H) similar to male but slightly shorter in proportion to anal somite and slightly wider at middle from dorsal view, about 2.7 times as long as wide (dorsal view); ornamentation and armature same as in male.

Antennula (Fig. 43I) seven-segmented, unornamented, relatively long, with slender aesthetasc on fourth segment, reaching beyond tip of appendage and more slender apical aesthetasc on seventh segment; setal formula (probably incomplete): 0.3.3.2.0.0.5. All setae smooth and slender. Length ratio of antennular segments, from proximal end, 1:2.2:1.5:1.1:0.5:0.7:1.8.

Antenna (Fig. 43J) relatively stout and long, composed of coxa (not drawn), allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 2.8 times as long as wide, and 1.4 times as long as endopod, unarmed and unornamented. Endopod about 3.6 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with one short spine and subapically with five strong and unipinnate elements. Exopod minute, cylindrical, about 3.1 times as long as wide, unornamented but armed with single unipinnate apical seta, about as long as segment.

Mandibula, maxillula, maxilla, and maxilliped unknown but probably similar to those of male.

First swimming leg (Fig. 43K) composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and two-segmented endopod. Exopod armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment,



Fig. 43. *Parastenocaris hinumaensis*. Male: A. anal somite and caudal rami, ventral view; B. antennula; C. second swimming leg; D. third leg; E fourth leg; F. fifth leg. Female: G. first two urosomal somites with fifth legs, ventral view; H. anal somite and caudal rami, dorsal view; I. antennula; J. antenna; K. first swimming leg; L. second swimming leg; M. third swimming leg; N. fourth swimming leg. Scales: A–F, H–N=20 μ m, G=unknown (cited from Kikuchi, 1970, modified).

about 3.4 times as long as wide and 1.5 times as long as second segment, unarmed, ornamented with single spinules on inner margin distally; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.6 times as long as entire endopod and 1.2 times as long as larger geniculate exopodal seta; all armature elements on ultimate endopodal and exopodal segmented strongly unipinnate along outer concave margin.

Second swimming leg (Fig. 43L) similar to that of male, but with proportionately longer and more slender first exopodal segment.

Third swimming leg (Fig. 43M) without clear demarcation between praecoxa, coxa, and basis; all being also unornamented. Basis armed with very long and smooth outer seta, about as long as first exopodal segment. Exopod two-segmented, ornamented with few large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, parallel with exopod, conical, armed with single seta on top fused to segment basally, unornamented.

Fourth swimming leg (Fig. 43N) without clear demarcation between praecoxa, coax, and basis; all being also unornamented and unarmed. Endopod one-segmented, ornamented with apical row of three spinules at base of apical spine, distinct at base, bipinnate, and slightly longer than endopod. Exopod similar to male, but with less outer ornamentation and straight.

Fifth leg (Fig. 43G) triangular, armed with four setae as in male, but with inner distal corner produced into spiniform process and shorter outermost (ancestral basal) seta.

Sixth legs (Fig. 43G) vestigial, not fused medially, covering gonopores, unornamented and unarmed.

TYPE: Type material probably lost.

TYPE LOCALITY: Japan, Ibaraki Prefecture, Lake Hinuma, Oyazawa (12 km south of Mito), interstitial from a sandy beach on the lake shore.

DISTRIBUTION: This species is only known from the type locality, Lake Hinuma, Ibaraki Prefecture, Japan, where it was collected on two separate occasions.

ECOLOGY: Interestingly, *P. hunumaensis* was collected from a lake interstitial during the coldest time of the year in Japan (January and February), with the water temperature being 6.2°C (Kikuchi, 1970). This would imply that the species may be a glacial relict in the fauna of Japan, but this would have to be checked by sampling there in all seasons and at different depths.

REMARKS: Kikuchi (1970) remarked that *P. hinumaensis* belongs to the *brevipes* group of species, resembling mostly *P. starretti*, *P. biwae* and *P. brevipes*. Reid (1995) synonymized *P. starretti* and *P. biwae* with *P. brevipes*. In this monograph we argue that at least *P. biwae* is a separate species. *Parastenocaris hinumaensis* differs from them, as well as from any other *Parastenocaris* species, by the shape and armature of the male fourth leg endopod and basal protrusions (Fig. 43E), shape of the male third leg (Fig. 43D), as well as by the shape and armature of the fifth legs in both sexes.

32. Parastenocaris irenae Enckell, 1970 (Fig. 44)

Parastenocaris irenae Enckell, 1970, p. 546, figs. 1-15.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 340 μ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of last two somites and caudal rami (Fig.

44A, B), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites smooth, very narrow, and difficult to distinguish from arthrodial membranes, especially dorsally. Integument weakly sclerotised, smooth, without surface ornamentation except sensilla and pores (no spinules or cuticular pits). Preanal somite (and probably three somites anterior to it) with large, oval dorsal cuticular window (Fig. 44A, B), constricted at middle. Anal somite 1.3 times as long as preanal somite, ornamented only with pair of large dorsal sensilla at base of anal operculum. Anal operculum (Fig. 44A) well developed, unornamented on outer surface, with almost straight caudal margin, almost reaching posterior end of anal somite, and representing 58% of somite width. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 44A, B) about 2.7 times as long as greatest width (dorsal view) and almost 0.7 times as long as anal somite, conical (slowly narrowing towards distal end), slightly divergent, with space between them almost 1.4 times one ramus width, armed with six armature elements (two lateral, one dorsal, and three apical), unornamented. Dorsal seta slender and smooth, inserted slightly posteriorly of midlength, somewhat closer to inner margin, about 0.9 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other, at 3/5 of ramus length. Proximal lateral seta inserted more dorsally, about twice as long as distal minute one, and about 0.7 times as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, slightly longer than ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta smaller than middle apical seta but also strong, also without breaking plane, smooth, about 1.6 times as long as ramus.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown, but presumably similar to those in type species.

Second swimming leg (Fig. 44C) composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and three elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, 3.4 times as long as greatest width, 1.7 times as long as endopod, with curved outer distal spine, slightly longer than segment. Endopod cylindrical and relatively slender, about 4.7 times as long as wide, reaching middle of first exopodal segment in length, ornamented with three large spinules along distal margin; armed apically with one smooth, slender inwards-pointing seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 44D) with smooth praecoxa and coxa. Basis robust, trapezoidal, unarmed, ornamented with five long spinules on outer margin and curved row of minute spinules on inner margin. Endopod absent. Exopod with both segments fused; ancestral proximal segment about 3.1 times as long as wide, with chitinous bulb on distal part of inner margin, ornamented with few spinules along outer margin distally, armed subapically with simple, strong, smooth and curved spine, 0.7 times as long as apophysis; ancestral distal segment (apophysis) much wider proximally, oriented inward, unornamented but with minute spiniform process apically, fused to segment; complex tridimensional structure of apophysis ends with membraneous bulbous part.

Fourth swimming leg (Fig. 44E) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process smaller, smooth and curved, simple spiniform structure, pointing inwards; outer process large and complex, pointing outward, fitting nicely into concave margin of first exopodal segment, and shielding proximal part of endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin proximally, but convex distally, three times as long as greatest width, with stout outer distal spine, 0.7 times as long as segment. Endopod one-segmented, inflated, about 0.6 times as long as first exopodal segment, pointing inwards, armed with single smooth seta apically (fused basally to segment), ornamented with two large spinules (both pointing outwards, but inner one fused basally to segment). Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 44F) simple triangular cuticular plate, inner distal margin produced posteriorly into long smooth spiniform process, ornamented with single spinule next to basal seta (or perhaps a minute seta?), armed with three smooth setae; outermost seta (ancestral basal one) longest, 1.7 times as long as entire leg and about 3.3 times as long as two other subequal setae (probably of endopodal origin).

Sixth legs unknown, probably very similar to type species.

Female: Body length same as in male, and presumably also habitus shape, ornamentation of somites, colour, and nauplius eye.

Genital double somite unknown. Anal somite and caudal rami same as in male. Antennula unknown, probably similar to type species. Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg probably similar to male.

Second swimming leg (Fig. 44G) also similar to male, but first exopodal segment with inner margin not concave (even slightly convex), and proportionately larger endopod.

Third swimming leg (Fig. 44G) composed of praecoxa, coxa, intercoxal sclerite, basis, two-segmented exopod, and one-segmented endopod. First exopodal segment rectangular, almost three times as long as wide, ornamented with four large spinules on outer margin, one spinule on outer distal corner, and hyaline frill distally on inner side; armed with stout and smooth outer spine, about 0.7 times as long as first exopodal segment. Endopod small and simple, fused basally to apical bipinnate spine, 0.9 times as long as first exopodal segment, straight.

Fourth swimming leg (Fig. 44I) without spiniform processes on basis. Endopod one-segmented, slender, curved slightly inwards, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, and about 0.9 times as long as endopod. Exopod similar to male, but first segment with straight inner margin.

Fifth leg (Fig. 44J) similar to male, but more elongated, with larger distal spiniform process; all setae also proportionately longer than in male, but armature basically same.

Sixth legs unknown but probably vestigial, fused into simple cuticular plate, covering gonopore; ornamentation and armature unknown.

TYPE: Type material lost.

TYPE LOCALITY: Sri Lanka, Northern Province, Per Aru, 14.5 km east of Mankulam, interstitial on banks of a small river.

DISTRIBUTION: Apart from the type locality (near Mankulam in Northern Province), the species was also collected from a small stream near Habarana in Central Province, Sri Lanka.

ECOLOGY: This species was collected in large numbers (45 males and 93 females) from coarse and very clean sands, on the banks of a small and slowly flowing river (1–3 m wide) from the type locality. Only three specimens were collected from coarse gravel on the banks of a small stream (1–2 m wide) in Central Province (Enckell, 1970). In both locations *P. irenae* lives sympatrically with an undescribed *Parastenocaris* species (*P.* sp.), which was represented by only one female in the type locality, whereas it was the dominant species in the second locality. This would imply that *P. irenae* shows a preference for smaller interstitial spaces, whereas in coarse gravel it becomes displaced by



Fig. 44. *Parastenocaris irenae*. Male: A. last two abdominal somites and caudal rami, dorsal view; B. last two abdominal somites and left caudal ramus, lateral view; C. basis, endopod, and first exopodal segment of second leg; D. third leg; E. basis, endopod, and first exopodal segment of fourth leg; F. fifth leg. Female: G. basis, endopod, and first exopodal segment of second leg; H. basis, endopod, and first exopodal segment of third leg; I. basis, endopod, and first exopodal segment of fourth leg; J. fifth leg. Scales: 50 μ m (cited from Enckell, 1970, modified).

the other species.

REMARKS: Presence of dorsal cuticular windows on anal somites and the shape of the fourth leg basis and endopod clearly place this species in the *brevipes* group of Lang (1948). In the original description, Enckell (1970) remarked that *P. irenae* resembles somewhat *P. longicauda* Chappuis (probably meaning *P. longicaudis* Chappuis, 1931), but since the latter was described only after females he was not able to draw further conclusions from this resemblance. He did not explain how the species differs morphologically from the other five Sri Lankan species described in the same paper. It differs easily from *P. noodti, P. singhalensis,* and *P. lanceolata* by the large distal spiniform process on the male fifth leg (Fig. 44F), absent in these three species. Two other Sri Lankan species have this process well developed: *P. brincki* and *P. curvispinus.* The latter species, however, belongs to a completely different group of species, as it has a completely different endopod of the male fourth leg. The former species is probably most closely related to *P. irenae*, but can be distinguished by longer anal somite and caudal rami, much shorter outer apical caudal seta, and a strong, pointed outer process on the first exopodal segment of the male third leg. Most other species-specific characters are found in the shape, armature and ornamentation of the male third and fourth legs, ornamentation of the anal somite, and small variations in the shape of the caudal rami.

33. Parastenocaris jane Karanovic, 2006 (Figs. 45–48)

Parastenocaris jane Karanovic, 2006, p. 204, figs. 101-104, 115A-C.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 501 μ m. Preserved specimen colourless. Nauplius eye absent. Habitus (Fig. 45A, F) cylindrical and very slender, without demarcation between prosome and urosome; prosome/ urosome ratio 0.7; greatest width at fourth pedigerous (third free) somite but very difficult to determine. Body length/width ratio about 8.4; cephalothorax 1.15 times as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally; thoracic, as well as abdominal, somites connected by well-developed arthrodial membranes. Integument not very strongly chitinised; simple large dorsal integumental window on genital and next three urosomites, cephalothorax with double dorsal window posteriorly (smaller window with thinner integument inside larger one). Pleural areas of cephalothorax and free pedigerous somites not well developed; cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Whole body, including caudal rami, covered by numerous small cuticular pits; only appendages, cuticular windows, and arthrodial membranes not covered by these pits. Rostrum small, membraneous, ornamented with two large dorsal sensilla, linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax (Fig. 45A) about 1.4 times as long as wide; representing 16% of total body length. Surface of cephalic shield and tergites of free pedigerous somites ornamented with several large sensilla. Hyaline fringe of all somites smooth.

Genital somite (Fig. 45A, F) ornamented with two sensilla dorsally and four sensilla laterally (two on each side), about 1.4 times as wide as long, with single, large, completely formed and longitudinally placed spermatophore (Fig. 45G) visible inside. Third urosomite ornamented with four dorsal, four lateral, and two ventral sensilla posteriorly. Fourth somite with two dorsal, four lateral (two on each side), and two ventral sensilla. Fifth urosomal (preanal) somite without visible ornamentation,



Fig. 45. *Parastenocaris jane*, Male. A. habitus dorsal view; B. mandibula; C. maxillula; D. maxilla; E. maxilliped; F. habitus, lateral view; G. urosome, ventral view; H. antenna. Scales: 100 μ m (cited from Karanovic, 2006, modified).

except for small cuticular pits that cover entire body. Anal somite ornamented with pair of large dorsal sensilla and one transverse row of spinules on inner side of anal operculum. Anal operculum (Fig. 46A) well developed, with somewhat concave and smooth distal margin, not reaching posterior end of anal somite, representing 63% of somite width. Anal sinus widely opened, with smooth ventral side and row of spinules on dorsal side (below anal operculum).

Caudal rami (Figs. 45G, 46A, E) about 2.9 times as long as greatest width (dorsal view), cylindrical (slightly narrowing towards distal end), divergent, with space between them equal to more than one ramus width; armed with six armature elements (two lateral, one dorsal, and three apical). Ornamentation consists of large cuticular pore laterally close to posterior margin and row of small spinules along posterior margin ventrally. Dorsal seta relatively long, inserted somewhat closer to inner margin at about 3/5 of ramus length, about 1.3 times as long as caudal ramus, biarticulate at base and smooth. Lateral setae thin and smooth, inserted close to each other, also at 3/5 of ramus length. Proximal lateral seta placed more dorsally, about 2.8 times as long as distal minute seta, and about 0.4 times as long as ramus. Inner apical seta small, smooth, inserted more ventrally, about 0.3 times as long as outer apical seta and 0.3 times as long as whole body. Outer apical seta small, also without breaking plane, and smooth, about 0.5 times as long as ramus.

Antennula (Fig. 46C) approximately as long as cephalothorax, eight-segmented, prehensile and strongly geniculate, unornamented. Proximal anterior corner of fifth segment and distal anterior corner of seventh segment protrude as strong spiniform processes, forming powerful pincers. Broad aesthetasc on fourth segment reaching tip of appendage. Much shorter apical aesthetasc on eighth segment. Setal formula: 0.6.4.2.4.0.0.8. All setae slender and almost all (except most proximal seta on second segment) smooth. Only one seta on second segment and one on third segment, articulating on basal part; one apical seta fused basally with apical aesthetasc.

Antenna (Fig. 45H) relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 2.8 times as long as wide, unarmed, ornamented with two short rows of large spinules along anterior surface and one cuticular pore near distal margin. Endopod about three times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two spines (proximal smooth and distal unipinnate) and apically with five strong and pinnate elements (two geniculate). Exopod minute, cylindrical, about 2.6 times as long as wide, unornamented but armed with single pinnate apical seta, about 1.6 times as long as segment.

Mandibula (Fig. 45B) with narrow cutting edge on elongated coxa, armed with one coarse tooth ventrally, one unipinnate seta dorsally, and several smaller teeth between. Palp one-segmented, cylindrical, about 2.8 times as long as wide, unornamented, and armed apically with two smooth and subequal setae.

Maxillula (Fig. 45C) with relatively small praecoxa, arthrite rectangular, long, unornamented, but armed with one slender anterior surface seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically, about 1.2 times as long as endite. Basis longer than coxal endite, armed with three apical smooth setae of about same length. Endopod and exopod absent.

Maxilla (Fig. 45D) with row of spinules and two endites on syncoxa; proximal endite armed apically with single smooth seta; distal endite twice as long as proximal one, armed apically with two smooth and one strong unipinnate seta. Basis drawn out into strong and smooth claw, without seta at base. Endopod represented by minute but distinct segment, armed with two smooth subequal apical setae.

Maxilliped (Fig. 45E) with unornamented short syncoxa; basis about 3.8 times as long as wide,



Fig. 46. *Parastenocaris jane*, Male. A. anal somite and caudal rami, dorsal view; B. fifth leg; C. antennula; D. fourth swimming leg; E. left caudal ramus, lateral view; F. third swimming leg; G. fourth swimming leg, different male; H. right caudal ramus, lateral view, different male; I. fifth leg, different male; J. third swimming leg, different male and different view. Scales: 100 μ m (cited from Karanovic, 2006, modified).

unornamented and unarmed; endopod represented by short curved claw, ornamented with row of spinules along concave side distally, about 0.8 times as long as basis.

First swimming leg with smooth coxa and intercoxal sclerite. Basis ornamented with few large spinules at base of outer spine and few spinules along distal margin, between endopod and exopod. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about 3.6 times as long as wide, unarmed, ornamented with large spinules along outer and inner margin; second segment armed apically with long geniculate seta and much shorter spine.

Second swimming leg with smooth coxa and intercoxal sclerite; basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about as long as exopod. Endopod one-segmented, linguiform, about 4.4 times as long as wide, reaching middle of first exopodal segment, ornamented with several spinules along apical margin, armed apically with one smooth seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 46F) with smooth praecoxa and intercoxal sclerite. Coxa ornamented with short row of spinules along distal margin, on both anterior and posterior surface. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin; inner margin bluntly serrated at middle. Endopod minute segment, basally fused to basis, unornamented, and armed apically with smooth seta, 4.6 times as long as segment. Exopod with both segments fused; ancestral proximal segment about 3.5 times as long as wide, with chitinous bulb on proximal part of inner margin and three long spinules near outer distal corner, armed subapically with strong, smooth and curved spine, reaching distal margin of apophysis; ancestral distal segment (apophysis) much smaller, oriented inward, unornamented, but armed with minute spine apically, which forms pincers with produced and blunt outer apical corner.

Fourth swimming leg (Fig. 46D) with smooth praecoxa, intercoxal sclerite and basis; coxa with few spinules near outer margin; basis armed with slender and smooth outer seta, inner-distal corner of basis produced into two large, heavily sclerotised, linguiform and blunt structures, longer one almost as long as endopod. Exopod three-segmented, ornamented with few large spinules along outer margin, and first and third segment with hyaline frills distally on inner side; first segment with concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta. Endopod one-segmented, about 0.4 times as long as first exopodal segment, claw-like, curved inwards, armed with single pinnate apical seta and ornamented with longitudinal row of five very long and slender spinules; middle part of endopod produced as separate smooth lobe, reaching distal margin of segment. Endopod and basal claws resembling powerful pincers.

Fifth leg (Fig. 46B) simple quadriform cuticular plate, ornamented with single large cuticular pore basally and armed with three smooth setae along distal margin; outermost seta (ancestral basal one) longest, about 4.5 times as long as other two subequal setae. Distal margin between outermost and other two setae produced posteriorly as small spiniform process. Fifth legs distinct at base (Fig. 45G) with space between them slightly less than two legs width.

Sixth legs (Fig. 45G) completely fused, forming single, smooth, large operculum covering gonopore, which represents 55% of genital somite width.

Female: Body length, excluding caudal setae, 390 μ m. Habitus (Fig. 47A), ornamentation of prosomites, colour, and nauplius eye similar to male.

Genital double somite (Figs. 47A, D, 48B) about as long as wide (ventral view), without trace of subdivision except for two ancestral integumental windows being partly fused into single large and complex one; ornamented with six posterior sensilla (two dorsal, two ventral, and two lateral) and two large dorsal sensilla anteriorly. Genital complex (Fig. 48B) occupying anterior ventral half of genital double somite; genital aperture paired, each closed off by small, unarmed operculum derived from vestigial sixth leg; median copulatory pore located anteriorly between genital apertures; seminal receptacles elongated, small; copulatory duct very short and well sclerotised. Third and fourth (preanal) somites similar to male. Anal somite ornamented additionally with two ventral pores (Fig. 47E) and two lateral ones (one on each side; Fig. 47D).

Caudal rami (Figs. 47E, D, 48C) similar to male but slightly shorter and with middle and outermost apical setae unipinnate.

Antennula (Fig. 48A) seven-segmented, unornamented, approximately as long as cephalothorax, with broad aesthetasc on fourth segment, reaching tip of appendage and more slender apical aesthetasc on seventh segment, fused basally to apical seta; setal formula: 0.4.5.2.1.0.9. Most-proximal seta on second segment unipinnate and articulating on basal part, all other setae smooth and without articulation or breaking plane. Length ratio of antennular segments, from proximal end, 1:2.5:1.5:0.8:0.7:1.4.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 47B), and second swimming leg (Fig. 47C) similar to male.

Third swimming leg (Fig. 48F) with smooth intercoxal sclerite and coxa; basis ornamented with large cuticular pore proximally and row of spinules near outer margin, armed with very long and smooth outer seta about as long as exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta. Endopod one-segmented, with ancestral apical spine completely fused to segment but still bipinnate; reaching 2/3 of first exopodal segment.

Fourth swimming leg (Fig. 48E) without spiniform processes on basis. Endopod one-segmented, ornamented with four large spinules at base of ancestral apical spine, fused to segment and bipinnate. Exopod similar to male.

Fifth leg (Fig. 48D) simple triangular cuticular plate, about twice as long as wide; ornamentation and armature similar to male but inner distal corner produced posteriorly into sharp and smooth, claw-like process, half as long as innermost and middle seta. Fifth legs separated medially, with space between them less than one leg width.

Sixth leg (Fig. 48B) small cuticular plate, covering gonopore, unornamented and unarmed.

TYPE: Type material deposited in the Western Australian Museum (WAM C34201-C34215).

TYPE LOCALITY: Australia, Western Australia, Pilbara region, Paraburdoo, bore hole.

DISTRIBUTION: Apart from the type locality (Paraburdoo), this species was originally described from a number of different localities in the Pilbara region of Western Australia (Karanovic, 2006). The species seems to be relatively widely distributed in this region, although it is endemic here.

ECOLOGY: All localities where this species was collected are bore holes in calcrete sediments, a characteristic geological formation in Western Australia, rich in calcium carbonate and full of holes and crevices, and thus an ideal habitat for stygofauna (Karanovic, 2006). The subterranean water temperature in this part of Western Australia is normally between 25 and 28°C throughout the year,



Fig. 47. *Parastenocaris jane*, Female. A. habitus, dorsal view; B. first swimming leg; C. second swimming leg; D. urosome, lateral view; E. anal somite and caudal rami, ventral view. Scales: 100 μ m (cited from Karanovic, 2006, modified).



Fig. 48. *Parastenocaris jane*, Female. A. antennula; B. genital double somite, ventral view; C. anal somite and caudal rami, dorsal view; D. fifth leg; E. fourth swimming leg; F. third swimming leg; G. fifth leg, different female; H. endopod of fourth swimming leg, different female; I. right caudal ramus, dorsal view, different female. Scales: 100 μ m (cited from Karanovic, 2006, modified).

but other environmental factors, such as dissolved oxygen, salinity, and conductivity, are highly variable (Karanovic, 2006).

REMARKS: Karanovic (2006) observed the following variable features in *P. jane*: body length of males ranges from 374 to 501 μ m, while in females it ranges from 356 to 492 μ m; small differences were noted in the appearance of the male third (Fig. 46F, J) and fourth (Fig. 46D, G) swimming legs; one male had a somewhat longer outer apical seta on the caudal rami (Fig. 46H); one female had a somewhat different endopod of the fourth swimming leg (Fig. 48H), as well as a much narrower fifth leg (Fig. 48G), also ornamented with two spinules on the produced inner distal corner; and one female had the principal apical seta on the caudal rami very short and swollen proximally (Fig. 48I). Parastenocaris jane also belongs to the brevipes group of species, having the characteristic endopodal complex of the male fourth leg; long distally serrate endopod of the female fourth leg; tapering caudal ramus with dorsal and lateral setae inserted around midlength; sixth legs in male fused into a single operculum; and bilobate female fifth leg. Karanovic (2006) noted that this species is relatively closely related to P. feuerborni and P. kimberleyensis, but it can be distinguished from both species by the shape of the male fourth leg endopod (armed apically with a spiniform element) and also by a different shape of the male third leg. Additionally, P. jane differs from P. kimberleyensis by a number of characters, including the presence of cuticular windows, ornamentation of the integument, and the shape of the inner basal processes on the male fourth leg. Unfortunately, the description of P. feuerborni is incomplete (see Chappuis, 1931, Lang, 1948), so many morphological details could not be compared. The pattern of integumental windows found in *P. jane* is probably among the most primitive ones and is found in many species of the *brevipes* group, as well as in *Simplicaris lethaea* Galassi and De Laurentiis, 2004, for example.

34. Parastenocaris kimberleyensis Karanovic, 2005 (Figs. 49-52)

Parastenocaris kimberleyensis Karanovic, 2005a, p. 361, figs. 34-63.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 0.5 mm. Preserved specimen colourless. Nauplius eye absent. Habitus (Fig. 49A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.9; greatest width at posterior end of cephalothorax, but not very obvious. Body length/width ratio about 8.3; cephalothorax just slightly wider than genital somite. Free pedigerous somites without expansions laterally or dorsally. Integument very weakly chitinised; integumental windows absent. Rostrum small, membraneous, unornamented, ovoid, reaching middle of first antennular segment, about as long as wide and not demarcated at base. Cephalothorax about 1.6 times as long as wide; representing 20% of total body length. Surface of dorsal shield covering cephalothorax ornamented with only few small sensilla. Tergites of free pedigerous somites also ornamented with few small spinules, except completely smooth first one. Hyaline fringes of all somites smooth. Genital somite ornamented with two small sensilla dorsally, about 1.5 times as wide as long, with single, large, completely formed, longitudinally placed spermatophore (Fig. 49A, B) visible inside. Third and fourth urosomal somites ornamented with pair of dorsal and ventral spinules each. Fifth urosomal (preanal) somite without visible ornamentation. Anal somite ornamented with pair of large dorsal sensilla, two ventral cuticular pores, and two short ventral rows of spinules at 1/3 of somite length. Anal operculum (Fig. 50C) strongly convex, smooth, not reaching posterior end of anal somite, representing 63% of somite width. Anal sinus smooth.

Caudal rami (Figs. 49A, 50C, D) long, cylindrical (slightly narrowing towards distal end), divergent, with space between them about two ramus width, and about 3.3 times as long as greatest width (ventral view); armed with six armature elements (two lateral, one dorsal, and three apical). Ornamentation consists of small cuticular pore laterally at anterior part. Dorsal seta relatively long, inserted somewhat closer to inner margin at about 2/3 of ramus length, about 1.3 times as long as caudal ramus, biarticulate at base and smooth. Lateral setae thin and smooth, inserted close to each other at 2/3 of ramus length. Proximal lateral seta placed more dorsally, about three times as long as distal one, and about 0.4 times as long as ramus. Inner apical seta small, smooth, about 0.5 times as long as ramus. Middle apical seta strongest, without breaking plane, bipinnate, about 6 times as long as outer apical seta and 0.4 times as long as whole body. Outer apical seta also without breaking plane, unipinnate along outer margin, about 0.8 times as long as ramus.

Antennula (Figs. 49C, 50F) 8-segmented, prehensile, not strongly geniculate, unornamented, approximately as long as cephalothorax. Broad aesthetasc on fourth segment reaching tip of appendage. Slender and short apical aesthetasc on eighth segment. Setal formula as follows: 0.5.5.2.4.0.0.9. Inner margin of fifth segment protruding into small spiniform process. One of the setae on third segment very short, spiniform (Fig. 49C). All setae smooth and without breaking planes. Only one seta on second segment articulating on basal part.

Antenna (Fig. 49D) relatively slender and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 3.3 times as long as wide, unarmed, and ornamented with two short rows of large spinules along anterior surface. Endopod about 2.8 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two spines and apically with five strong armature elements (two of which are geniculate). Exopod minute, cylindrical, about three times as long as wide, unornamented, armed with only one bipinnate apical seta, about 2.3 times as long as segment.

Mandibula (Fig. 50A) with narrow cutting edge on elongated coxa, armed with three coarse teeth ventrally, one smooth seta dorsally, and several smaller teeth between. Palp one-segmented, cylindrical, about three times as long as wide, unornamented, and armed apically with two smooth and subequal setae.

Maxillula (Fig. 50E) with relatively small praecoxa, arthrite of rectangular, long, unornamented, and armed with one strong anterior surface setae, and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth armature element apically, about 1.5 times as long as endite. Basis longer than coxal endite, armed with three apical smooth armature elements of about same length. Endopod and exopod completely reduced.

Maxilla (Fig. 50B) with two endites on syncoxa; proximal one armed apically with only one bipinnate seta; distal endite twice as long as proximal one, armed apically with two smooth and one strong unipinnate seta. Basis fused basally with syncoxa, drawn out into strong claw, without seta at base. Endopod represented by minute but distinct segment, armed with two smooth subequal apical setae.

Maxilliped (Fig. 50G) with unornamented short syncoxa; basis about three times as long as wide, unornamented and unarmed; endopod represented by short curved claw, ornamented with row of spinules along concave side distally, about 0.7 times as long as basis.

First swimming leg (Fig. 51A) with smooth coxa and intercoxal sclerite. Basis ornamented with few large spinules at base of outer spine. Exopod three-segmented, armed with one outer spine on


Fig. 49. *Parastenocaris kimberleyensis*, Male. A. habitus, dorsal view; B. urosome, ventral view; C. antennula, with enlarged detail of third segment armature; D. antenna, without distal part of endopod; E. rostral area, dorsal view. Scales: 100 μ m (cited from Karanovic, 2005, modified).

first segment and four armature elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments. Endopod twosegmented, somewhat longer than exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about 3.4 times as long as wide, unarmed, ornamented with few large spinules along outer margin and one long row of large spinules along inner margin; second segment



Fig. 50. *Parastenocaris kimberleyensis*, Male. A. mandibula; B. maxilla; C. anal somite and caudal rami, dorsal view; D. anal somite and left caudal ramus, lateral view; E. maxillula; F. antennula; G. maxilliped. Scales: 100 μ m (cited from Karanovic, 2005, modified).

armed apically with long geniculate seta and much shorter spine.

Second swimming leg (Fig. 51B) with smooth coxa and intercoxal sclerite; basis unarmed, ornamented with row of large spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long armature elements (probably outer spine and two apical setae), innermost one about 1.3 times as long as exopod. Endopod one-segmented, linguiform, reaching middle of first exopodal segment, ornamented with several spinules along apical margin, armed apically with 1 smooth seta, about 1.5 times as long as segment.

Third swimming leg (Fig. 51C) with smooth praecoxa, coxa and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with longitudinal row of very large spinules along distal part of inner margin (distalmost strongest) and diagonal row of spinules close to outer margin. Endopod minute, one-segmented, smaller than largest spinule on inner margin, unornamented and armed apically with smooth seta, twice as long as segment. Exopod with both segments fused; ancestral proximal segment about four times as long as wide, somewhat swollen at distal part of inner margin, armed subapically with strong, short, smooth and curved spine, which reaches middle of apophysis; ancestral distal segment (apophysis) much smaller, oriented inward, unarmed and unornamented, terminating in U-shaped thin chitinous structure.

Fourth swimming leg (Fig. 51D) with smooth coxa, intercoxal sclerite and basis; basis armed with slender and smooth outer seta, inner-distal corner of basis produced into two large, heavily sclerotised claws, longer one almost as long as endopod. Exopod three-segmented, ornamented with few large spinules along outer margin, and first and third segment with hyaline frills distally on inner side; first segment with swollen distal part of inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta. Endopod one-segmented, about 0.6 times as long as first exopodal segment, claw-like, curved inwards, unarmed and ornamented with longitudinal row of very long and slender spinules. Endopod and basal claws resembling powerful pincers.

Fifth leg (Fig. 51E) simple semitrapezoidal cuticular plate, unornamented and armed with three smooth setae along distal margin; outermost seta (ancestral basal one) longest, about four times longer than median one (slightly shorter than plate) and about 6.5 times as long as innermost seta. Fifth legs distinct at base (Fig. 49B) with space between them about equal to two leg widths.

Sixth legs (Fig. 49B) completely fused, forming single large operculum covering gonopore, which represents 80% of genital somite width, ornamented with transverse row of spinules along posterior margin and unarmed.

Female: Body length, excluding caudal setae, 0.473 mm. Habitus, ornamentation of prosomal somites, colour, and nauplius eye similar to male. Genital double-somite (Fig. 52K) about as long as wide (ventral view), without trace of subdivision, ornamented only with six posterior sensilla (two dorsal, two ventral and two lateral). Genital complex (Fig. 52F) occupying anterior ventral half of genital double somite, with two very closely set copulatory pores, with only one cuticular ridge between them, situated in copulatory funnel between sixth legs; copulatory duct not clearly visible inside somite; seminal receptacles trapezoidal, small; single genital aperture covered with single large operculum formed by fused and reduced sixth leg, which represents about 70% of somite width. Caudal ramus (Fig. 52J), antenna (Fig. 52I), mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 52A), and second swimming leg (Fig. 52C) similar to male.

Antennula (Fig. 52D) seven-segmented, unornamented, approximately as long as cephalothorax, with broad aesthetasc on fourth segment, reaching middle of seventh segment, and more slender apical aesthetasc on seventh segment, fused basally to apical seta; setal formula as follows: 0.5.5.2.1.0.9. Proximalmost seta on second segment and 1 seta on seventh segment articulating on basal part; all setae smooth and without breaking plane. Length ratio of antennular segments, from proximal end, 1:2.6:1.5:1.6:0.8:0.9:1.5.

Third swimming leg (Fig. 52B) with smooth intercoxal sclerite; coxa and basis ornamented with row of spinules near outer margin; basis armed with long and smooth outer seta, about 0.7 times



Fig. 51. *Parastenocaris kimberleyensis*, Male. A. first swimming leg; B. second swimming leg; C. third swimming leg; D. fourth swimming leg; E. fifth leg; F. basis, endopod and first exopodal segment of fourth swimming leg, different male; G. second swimming leg, different male. Scales: 100 μ m (cited from Karanovic, 2005, modified).

as long as exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second segment armed with outer spine and apical strong seta. Endopod one-segmented, with ancestral apical spine completely fused to segment, but still bipinnate; reaching 2/3 of first exopodal segment.

Fourth swimming leg (Fig. 52E, G) with first exopodal segment with inner margin straight and



Fig. 52. *Parastenocaris kimberleyensis*, Female. A. first swimming leg; B. third swimming leg; C. endopod of second swimming leg; D. antennula; E. endopod of fourth swimming leg; F. genital area, ventral view; G. first exopodal segment of fourth swimming leg; H. fifth leg; I. antenna; J. right caudal ramus, lateral view; K. fifth pedigerous and genital double-somite, lateral view. Scales: 100 μ m (cited from Karanovic, 2005, modified).

without spiniform processes on basis. Endopod one-segmented, with ancestral apical spine fused to segment, with three large spinules at its base and unipinnate along inner margin. Other details similar to male.

Fifth leg (Fig. 52H, K) bilobate simple cuticular plate, ornamented with cuticular pore at base of outer (basal) lobe and with ring of spinules around acute extension of inner (endopodal) lobe. Basal lobe armed with long basal seta and small spine (or perhaps spinule); inner lobe armed with two smooth and much shorter setae on outer margin (probably ancestral exopodal armature). Fifth legs separated medially, space between them less than one leg width.

Sixth legs (Fig. 52F) completely fused, small cuticular plates, forming single large operculum covering gonopore, unornamented and unarmed.

TYPE: Type material deposited in the Western Australian Museum (WAM C28624-C28627).

TYPE LOCALITY: Australia, Kimberley region, Argyle Diamond Mine, bore hole.

DISTRIBUTION: This species is known only from the type locality, a bore hole at the Argyle Diamond Mine in the Kimberley region of Western Australia. Apparently the species is a short-range endemic, like so many other Western Australian subterranean copepods (Karanovic, 2004, 2006).

ECOLOGY: Little is known about this species' habitat preferences, other than it is most probably a stygobiont. Subterranean water temperatures in that part of Australia are normally in high twenties or low thirties.

REMARKS: Karanovic (2005a) recorded some variable features in this species. Body lengths of males ranged from 408 to 500 μ m. One male was observed with comparatively longer spines on the second swimming leg (Fig. 51G) and with smaller basal processes on the fourth swimming leg (Fig. 51F), although they are drawn in slightly different positions than those in the holotype. *Parastenocaris kimberleyensis* belongs to the *brevipes* group of species, which was defined by Lang (1948) and named after the type species of the genus. Karanovic (2005a) compared this species with all 16 members of the group known at that time, and provided a key to 14 species that he considered as valid members. He also remarked that the presence of this group in northern part of Australia may suggest their relatively recent arrival, if the hypothesis of the origin of this group in tropical Asia (Reid 1995) is correct.

35. Parastenocaris koreana Karanovic and Lee, 2012 (Figs. 53–60)

Parastenocaris brevipes Kessler: Lee and Chang, 2009: p. 176, fig. 6; Chang, 2009, p. 225, fig. 96; Chang, 2010, p. 91, fig. 41.

Parastenocaris koreana n. sp.: Karanovic and Lee, 2012.

Male: (based on holotype male, numerous paratypes and several specimens from two other localities). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 395 to 539 μ m (437 μ m in holotype). Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites (first pedigerous fused to cephalothorax)), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Podoplean boundary between prosome and urosome inconspicuous. Habitus (Figs. 53A, 55A, F, 57A, 59A) cylindrical and very slender, without any demarcation between prosome and urosome; prosome/urosome ratio about 0.7 in



Fig. 53. *Parastenocaris koreana*. Male 1 (all from Wangpi Stream): A. habitus, dorsal view; B. first four urosomal somites, dorsal view; C. anal somite and caudal rami, dorsal view; D. antennulae, dorsal view. Female 1: E. fifth pedigerous and genital double somites. Female 2: F. fifth pedigerous and genital double somites. Scales: $A=100 \mu m$, $B-F=10 \mu m$ (All SEM micrographs original).



Fig. 54. *Parastenocaris koreana*. Female 3 (all from Wangpi Stream): A. habitus, lateral view; B. cephalothorax, lateral view; C. anal somite and right caudal ramus, lateral view. Female 3: D. anal somite and caudal rami, ventral view. Female 2: E. mouth appendages, ventral view; F. mouth appendages, detail, ventral view. Scales: A=100 μ m, B-E=10 μ m, F=1 μ m (All SEM micrographs original).

dorsal view; greatest width in dorsal view at posterior end of cephalothorax but hard to establish (fourth pedigerous somites only slightly narrower); free prosomal somites in lateral view slightly narrower than cephalothorax or urosome. Body length/width ratio about 9.6; cephalothorax 1.07 times as wide as genital somite. Free pedigerous somites without any lateral or dorsal expansions, all connected by well developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and hard to distinguish from arthroidal membranes (Fig. 53B), especially dorsally, except in preanal somite, where hyaline fringe well developed (Figs. 53A, 59A). Integument weakly sclerotized, smooth but covered with very shallow pits on all somites and caudal rami (sometimes hardly visible), ornamented only with sensilla and pores (no spinules, except on posterior margin of caudal rami ventrally), with round dorsal double cuticular window on cephalothorax (Figs. 57C, 59A), trapezoidal simple dorsal cuticular window on genital, and elongated simple dorsal windows on three postgenital somites (Fig. 59A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view (Figs. 55A, B, 57A).

Rostrum (Figs. 58A, 59A) small, membranous, not demarcated at base, ornamented with two large dorsal sensilla (No. 1), linguiform, not reaching distal margin of first antennular segment, about as long as wide.

Cephalothorax (Figs. 55B, 57C, 59A) about 1.8 times as long as wide in dorsal view; representing 19% of total body length. Surface of cephalic shield ornamented with 16 pairs of large sensilla (all homologous with sensilla in *P. young* and assigned same Arabic numerals); with dense pattern of shallow cutical pits of different sizes; five pairs of sensilla surround double cuticular window, but its surface without pits; anterior lateral corners of outer window with short sutures pointing antero-lateally. Athroidal membrane between cephalothorax and second pedigeous somite (first free) wider than between any other somites, with one large and many smaller folds and wrinkles.

Second pedigerous somite (= first free somite) (Figs. 55B, 57C, 59A) slightly narrower than posterior half of cephalothorax in dorsal view, with four pairs of large sensilla (three dorsal and one lateral; Nos. 17–20), and with small unpaired dorsal pore in anterior half.

Third pedigerous somite (Fig. 59A) slightly wider and shorter than second pedigerous, with four pairs of large sensilla (Nos. 21–23 and 25), also with unpaired dorsal pore; note: sensilla pair No. 24 missing (present in *P. young*).

Foruth pedigerous somite (Fig. 59A) slightly narrower and considerably longer than third pedigerous somite in dorsal view, with only three pairs of large posterior sensilla (Nos. 26–28), with cemicircular sutures in anterior part dorsally and unpaired cuticular pore in between them.

First urosomite (= fifth pedigerous somite) (Fig. 59A) slightly narrower and shorter than fourth pedigerous somite, also with three pairs of large posterior sensilla (Nos. 29–31), but without arched dorsal sutures or cuticular pores.

Second urosomite (= genital somite) (Fig. 59A, B) slightly wider and longer than first urosomite, about 1.1 times as wide as long in ventral view, with triangular small cuticular window in anterior half, also with three pairs of posterior sensilla (Nos. 32–34), but dorsal pair (No. 32) closer to each other than in first urosomite; single longitudinally placed spermatophore inside anterior half of somite about as long as somite.

Third urosomite (Figs. 53B, 59A,) about as long and as wide as second urosomite, but with shorter and much wider dorsal cuticular window, also with three pairs of large posterior sensilla (Nos. 36, 37 and 39); sensilla Nos. 35 and 38 missing (present in *P. young*).

Foruth urosomite (Figs. 53B, 59A) with slightly larger dorsal cuticular window and slightly longer, but as wide as and with similar ornamentation, consisting of only three pairs of large posterior sensilla (Nos. 41, 42 and 44); sensilla Nos. 40 and 43 missing (present in *P. young*).



Fig. 55. *Parastenocaris koreana*. Holotype male (all from Imjin River): A. habitus, lateral view; B. cephalothorax, lateral view; C. anal somite and left caudal ramus, lateral view; D. left antennula, lateral view; E. third and fourth swimming legs, lateral view. Paratype male 1: F. habitus, ventral view. Scales: A, F=100 μ m, B-E=10 μ m (All SEM micrographs original).



Fig. 56. *Parastenocaris koreana*. Paratype male 1 (all from Imjin River): A. third and fourth swimming legs, ventral view. Allotype female: B. habitus, lateral view. Paratype female 1: C. anal somite and caudal rami, ventral view; D. fifth pedigerous and genital double somite. Scales: A, C, D=10 μ m, B=100 μ m (All SEM micrographs original).

Fifth urosomite (= preanal somite) (Figs. 53A, 55A, F, 57A, 59A) slightly narrower and shorter than fourth urosomite, with largest dorsal cuticular window of all urosomites, and without any surface ornamentation; hyaline fringe well defined on all sides.

Sixth urosomite (= anal somite) (Figs. 53C, 55C, 57D, 59A, C) about 1.4 times as long as and 0.9 times as wide as preanal somite, ornamented with pair of large dorsal sensilla at base of anal operculum (No. 45), pair of large lateral cuticular pores in anterior half, and pair of ventral pores at base of caudal rami (no spinules on ventral surface), in addition to numerous shallow cuticular pits. Anal operculum well developed, unornamented on outer surface, with smooth and deeply concave distal margin, not reaching posterior end of anal somite, representing 58% of somite's width. Anal sinus wide opened, ornamented with two long diagonal rows of slender spinules on ventral side, and one additional row on dorsal side (inner side of anal opeculum).

Spermatophore (Fig. 59D) about 2.5 times as long as wide, kidney-shaped, with long and narrow,



Fig. 57. *Parastenocaris koreana*. Male 1 (all from Daehwa Stream): A. habitus, lateral view; B. anal somite and right caudal ramus, lateral view. Male 2: C. cephalothorax and antennulae, dorsal view; D. anal somite and caudal rami, dorsal view. Scales: A=100 μ m, B-D=10 μ m (All SEM micrographs original).

distally curved neck.

Caudal rami (Figs. 53C, 55C, 57B, D, 59A, C) slender, about 3.2 times as long as greatest width (ventral view) and about half as long as anal somite, cylindrical but tapering towards posterior end, slightly divergent, with space between them about 1.6 times of one ramus width; armed with seven elements (three lateral, one dorsal, and three apical). Ornamentation consists of large lateral cuticular pore at about 2/3 of ramus langth, and posterior ventral row of several spinules along posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at midlength, about 0.9 times as long as caudal ramus, triarticulate basally (inserted on two pseudo-joints). Lateral seta slender and smooth, inserted very close to each other also at midlength, two larger ones more anteriorly and minute one in between and more posteriorly. Anterior lateral seta which inserted more dorsally longest, 0.7 times as long as ramus, 2.5 times as long as ventral anterior seta, and about five times as long as minute (distal) seta. Inner apical seta smooth, inserted close to ventral margin,

about 0.8 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 3.6 times as long as ramus, pointing posteriorly but curled midlength. Outer apical seta also without breaking plane and smooth, relatively strong basally but much shorter, about 1.3 times as long as ramus, inserted close to dorsal surface and pointing latero-posteriorly.

Antennula (Figs. 53D, 55D, 57C, 58A, 59E) slightly shorter than cephalothorax, slender, eightsegmented, prehensile and strongly digeniculate, ornamented with arched row of ventral spinules on first segment distally, and with ribbed elongated chitinous plate on anterior surface of sixth segment. First segment very short, while second longest. Geniculation between third and fourth and between sixth and seventh segments; last two segments at 90° angle. Distal anterior corner of seventh segment produced into very small spiniform process, but larger proximal spiniform process present on fifth segment on anterior surface. Long aesthetasc on fifth segment reaching beyond tip of appendage for length of last segment, fused basally to slightly longer seta, relatively slender and blunt distally; much shorter and more slender apical aesthetasc on seventh segment, fused basally to two setae (acrotheck). Setal formula: 0.6.4.2.4.0.1.9. All setae slender and all, except largest seta on second segment, smooth; most setae with pore on tip; proximallmost seta on second segment unipinnate with several long spinules along anterior surface, much shorter than two large setae on fifth segment or longest apical seta on eighth segment (latter probably longest); only seta on eighth segment minute.

Antenna (Figs. 55B, 58A, 59F) relatively stout and short, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unarmed, ornamented with three short spinules. Allobasis about three times as long as wide, unarmed but ornamented with two rows of large spinules on anterior surface. Endopod 0.8 times as long as allobasis and tnearly three times as long as wide, with two parallel surface frills subdistally, ornamented with large spinules along anterior surface, armed laterally with two short spines (proximal one shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about twice as long as wide, unornamented but armed with single apical seta, which 2.6 times as long as segment. All antennal armature unipinnate.

Labrum (Fig. 55B) large and triangular in lateral view, with narrow and straight cutting edge, without any ornamentation on anterior surface, with several parallel rows of spinules along narrow cutting edge (three on outer distal corners strongest and very wide).

Paragnaths (Fig. 55B, F) strongly fused into trilobite structure, with numerous distal rows of slender short spinules on lateral lobes, one distal row of minute spinules on central lobe, and another transverse row of 14 very long spinules on posterior surface of central lobe at about 2/3 of its length.

Mandibula (Fig. 55B) with narrow cutting edge on elongated coxa, armed with one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules in between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on tip.

Maxillula (Fig. 55B) with relatively large praecoxa, arthrite rectangular, about 1.5 times as long as wide from lateral view, ornamented with single spinule on posterior surface near dorsal margin, armed with lateral strong seta and four apical elements (probably three spines and one strong seta; apical spines with crown of spinules on tip, resembling small hands). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with three apical setae (two smooth and slender, one curved and unipinnate), and single minute lateral seta. Endopod and exopod absent (fused to basis without trace), minute seta on basis probably representing remnants of exopodal armature. All coxal and basal setae, as well as smooth lateral seta on praecoxa, with pore on tip.



Fig. 58. *Parastenocaris koreana*. Male 1 (all from Daehwa Stream): A. antennulae, lateral view. Female 1: B. habitus, lateral view. Female 2: C. mouth appendages, ventral view. Female 3: D. fifth pedigerous and genital double somite. Scales: A, C, D=10 μ m, B=100 μ m (All SEM micrographs original).

Maxilla (Fig. 55B) composed of syncoxa, basis, and one-segmented endopod, ornamented with row of five spinules on inner side of syncoxa proximally, and with arched row of six spinules on posterior side of suncoxa close to outer margin. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with two smooth and one pinnate seta apically. Basis drawn out into strong and unipinnate claw, without seta at base, with cuticular pore on convex margin near distal tip. Endopod represented by minute segment, armed with two smooth subequal apical setae. All setae on maxilla with pore on tip.

Maxilliped (Fig. 55B) with short and relatively strong syncoxa, unarmed and unornamented; basis slender, almost five times as long as wide and three times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, ornamented with several strong spinules along concave margin distally, about 0.7 times as long as basis.

First swimming leg (Figs. 55B, F, 57A) with unarmed praecoxa, coxa, and intercoxal sclerite. Inter-

coxal sclerite very small, with narrow and concave distal margin and smooth. Paecoxa ornamented with several rows of minute spinules on anterior surface. Coxa with posterior row of large spinules on posterior surface and close to outer margin. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, another bunch along distal margin at base of endopod, and several long spinules on inner margin proximally; armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin and distally on all segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on anterior surface along distal margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.3 times as long as entire endopod, 1.2 times as long as larger geniculate exopodal seta, and twice as long as outer spine on endopod. All exopodal armature unipinate along outer margin.

Second swimming leg (Figs. 55B, F, 57A, 59G) with smooth praecoxa and intercoxal sclerite. Intercoxal sclerite large, trapezoidal, with deeply concave distal margin. Praecoxa triangular and large. Coxa short, rhomboidal, with diagonal row of small spinules on anterior surface and two shorter rows of spinules along distal margin on posterior surface. Basis larger than coxa, semicircular, unarmed, ornamented with row of spinules on outer margin and another arched row of spinules at base of endopod. Exopod three-segmented, ornamented with large spinules along outer margin, and with distal hyaline frills on each segment on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost element 1.3 times as long as entire exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and slender, 5.8 times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along as segment and pointing inwards.

Third swimming leg (Figs. 55E, 56A, 59H-J) with smooth intercoxal sclerite, which largest of all legs, trapezoidal, and with short and concave distal margin. Praecoxa not well defined on anterior surface, triangular on posterior surface, about as large as in second leg, unarmed and unornamented. Coxa rectangular, with arched row of large spinules on anterior surface, and two rows of spinules along posterior margin on posterior surface (outer minute). Basis robust, ornamented with long row of large spinules and one pore on anterior surface, armed with outer long and slender seta; distal inner corner of basis produced distally as bulbous soft semicircular lobe, smaller than in P. biwae. Endopod represented with single smooth and minute armature element, inserted on inner margin at 3/4 of basis length, shorter but stronger than spinules on anterior sruface. Exopod with both segments fused; ancestral proximal segment 2.7 times as long as wide, curved inwards and with thin hyaline lamelle along inner margin, and three strong and short chitinous beakes on posterior surface, ornamented with two or three minute spinules on distal outer corner; armed subapically with simple, strong, smooth and inwardly curved spine, which about as long as apophysis and more or less flat distally; ancestral distal segment (apophysis) cylindrical, oriented slightly inwards, ornamented with single pore on anterior surface; armed with single short element on top, which leaf-like, with very thin cuticulum, more or less ovoid.

Fourth swimming leg (Figs. 55E, 56A, 59K) with smooth praecoxa and intercoxal sclerite. Intercoxal sclerite shorter and smaller than in third, with equally long and concave distal margin. Praxoca



Fig. 59. *Parastenocaris koreana*, Paratype male 2 (from Imjin River). A. habitus dorsal view; B. genital somite, ventral view; C. anal somite and caudal rami, dorsal view; D. spermatophore; E. antennula, ventral view; F. exopod of antenna; G. encopod of second swimming leg, anterior view; H. third swimming leg, anterior view (undissected); I. third swimming leg, posterior view; J. tip of third swimming leg, posterior view; K. fourth swimming leg without last two exopodal segemnts, posterior view. Arrows indicating features different from P. biwae. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 100 μ m.

small and triangular. Coxa rhomboidal, slightly larger than in second leg, unarmed, ornamented with short distal row of minute spinules on posterior surface. Basis large and more or less rectangular, armed with single smooth outer seta, ornamented with two minute spinules on outer margin at base of outer seta, and with three huge chitinous spiniform process on inner distal corner; anterior process bilobate distally and very wide; inner process spiniform and curved outward, longest; posterior process shortest but most strongly chitinized. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with strongly concave and smooth inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and long and strong apical seta; apical seta about as long as entire exopod, and more than twice as long as outer spine. Endopod one-segmented, narrower but longer than first exopodal segment, cylindrical proximally and bilobate distally, with inner lobe somewhat longer and stronger, ornamented with several strong spinules (although not as long as in *P. biwae*); inner lobe with thin cuticulum and with several minute spinules along distal margin.

Fifth leg (Fig. 55F) simple short cuticular plate, almost rectangular in shape, ornamented with single pore on anterior surface and single spinule at base of outermost seta, armed with three smooth setae; outermost seta (ancestral basal one) longest, almost three times as long as entire leg; middle seta (probably ancestral outer endopodal) much shorter, 1.5 times as long as leg, and 1.3 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with small space between them, pointing caudally, not reaching distal margin of fifth pedigerous somite.

Sixth legs (Fig. 59B) smooth, unarmed and unornamented, forming simple lage operculum covering gonopore, probably both fused together or right one reduced and left one enlarged, representing 62% of somite's width.

Female: (based on allotype female, many paratypes and several specimens from two other localities). Body length, excluding caudal setae, from 403 to 443 μ m (432 μ m in allotype). Habitus (Figs. 54A, 56B, 58B), ornamentation of prosomites, colour and nauplius eye similar to male, except genital and first abdominal somite fused into double somite and habitus slightly less slender.

Genital double somite (Figs. 53E, F, 56D, 58D, 60A, B) about 1.2 times as long as wide (ventral view), without any trace of subdivision, with oval dorsal cuticular window in anterior half, which much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures covered by vestigial sixth legs; median copulatory pores also partly covered by fused sixth legs; seminal receptacles small, ovoid, with strongly sclerotized outer wall and weakly sclerotized other walls; copulatory duct very short and weakly sclerotized. All posterior senislla homologous to those on male third urosomite, while all sensilla from male second urosomite missing except lateral pair (No. 33).

Third, fourth (preanal), and fifth (anal) urosomites very similar to male (Figs. 54A, D, 56B, C, 58B, 59A, B).

Caudal rami (Figs. 54C, D, 56C, 59A, B) slightly shorter in proportion to anal somite, about three times as long as wide in ventral (or dorsal) view, and slightly less divergent, but also cylindrical and armed and ornamented as in male.

Antennula (Figs. 54A, B, 56B) seven-segmented, ornamented on first segment with few minute spinules on ventral surface, not geniculate, with slender aesthetasc on fourth segment, not reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, which fused basally to two apical setae; proximal aesthetasc much more slender than in male; setal formula: 0.4.5.2.1.0.9. All setae, except proximalmost one on second segment, smooth, and most setae with pore on tip.

Antenna (Fig. 58B), labrum (Figs. 54E, F, 58C), paragnaths (Figs. 54E, F, 58C), mandibular (Figs. 54E, F, 58C), maxillula (Figs. 54E, F, 58C), maxilla (Figs. 54E, F, 58C), maxilliped (Figs. 54E, 58C), first swimming leg (Figs. 54A, B, E, 56B, 58B, C), and second swimming leg (Fig. 54A, 56B, 58B, 60C) same as in male.

Second swimming leg (Fig. 60C) with proportionately less elongated endopod.

Third swimming leg (Fig. 60D) with smooth praecoxa and intercoxal sclerite. Coxa with three large spinules on anterior surface, and two rows of spinules along distal margin on posterior surface, unarmed. Basis ornamented with several large spinules on outer margin distally, armed with very long and smooth outer seta, which 0.9 times as long as entire exopod. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate; apical seta 1.3 times as long as entire exopod. Endopod one-segmented, small, cylindrical and unornamented, armed with apical spiniform bipinnate element on tip, which basally fused to segment, reaching posterior margin of first exopodal segment in length.

Fourth swimming leg (Fig. 60E) without spiniform processes on basis, with row of spinules at base of endopod. Endopod one-segmented, slender and long, cylindrical, straight, ornamented with apical row of four large spinules at base of apical spine (no lateral spinules on inner margin); apical spine not distinct at base, bipinnate and robust, and about 0.9 times as long as endopod; endopod with apical spine reaching midlength of third exopodal segment in length. Exopod similar to male, but inner margin of first exopodal segment not as much concave; apical seta as long as entire exopod.

Fifth leg (Figs. 53E, F, 56D, 58D, 60F) also simple cuticular plate, but with inner distal corner produced into strong and blunt spiniform process, which about 1.2 times as long as rest of leg (proportionately shorter than in *P. biwae*), not reaching in length tips of innermost seta; armature and ornamentation same as in male; spinule at base of outermost seta smaller than in *P. biwae*.

Sixth legs vestigial (Figs. 53E, F, 56D, 58D, 60B), narrowly fused into simple cuticular flap, covering gonopore, unornamented and unarmed; distal margin thin, medial part very short, lateral part longer and bilobate, each lobe terminating into more or less sharp tip, but shae and length of lobes and apical tips variable.

TYPE LOCALITY: South Korea, Gyeonggido region, Paju city, Jeokseong town, Imjin river, interstitial, 37° 59'04.4"N 126° 55'41.2"E.

DISTRIBUTION: This species seems to be widely distributed in South Korea. Lee and Chang (2009) and Chang (2009, 2010) reported it (as *P. brevipes*) from seven different localities. We add three new localities here.

ECOLOGY: Specimens were obtained only from interstitial on river banks, and no records from caves, wells or other subterranean habitats exist. The species was never recorded in surface water habitats, so it is probably an obligate subterranean water dweller (stygobiont).

SPECIMEN EXAMINED: Types: holotype male, paratype female and four paratypes (two males and two females) on one SEM stub (NIBRIV0000232646); three paratype males and two paratype females dissected on one slide each (NIBRIV0000232647–NIBRIV0000232651); one paratype male on one slide in toto (NIBRIV0000232652); 20 paratypes (eight males+12 females) together in 99% ethanol, sample No. 6 (NIBRIV0000232653); another 15 paratypes (four males+seven females+four copepodids) together in 99% ethanol, sample No. 3 (NIBRIV0000232654); another seven paratypes (3 males+4 females) together in 99% ethanol, sample No. 3 (NIBRIV0000232655); and another six paratype males together in 99% ethanol, sample No. 5 (NIBRIV0000232656); all collected at type locality, 14 July 2010, leg. J.-L. Cho.



Fig. 60. *Parastenocaris koreana*, Paratype female 2 (from Imjin River). A. urosome, lateral view; B. urosome, ventral view; C. endopod of second swimming leg, anterior view; D. third swimming leg, anterior view; E. fourth swimming leg, anterior view; F. fifth legs, anterior view. Arrows indicating features different from *P. biwae*. Arabic numerals indicating pairs of sensilla homologous to those in *P. young*. Scales: 100 μ m.

Other material: Three males and four males on one SEM stub (NIBRIV0000232654); 12 specimens (four males+3 females+5 copepodids) together in 99% ethanol, sample No. 4 (NIBRIV0000232657); another five specimens (two males+three females) together in 99% ethanol, sample No. 4 (NIBRIV 0000232658); another male in 99% ethanol, sample No. 17 (NIBRIV0000232659); South Korea, Gyung-sangbuk-do region, Uljin city, Geunnam town, Wangpi stream, interstitial from several beaches on banks, 36° 57′41.4″N 129° 22′46.4″E, 18 May 2010, leg. J.-L. Cho.

Three males and three females on one SEM stub (NIBRIV0000232660); 10 specimens (three males+ four females+three copepodids) together in 99% ethanol, sample No. 12 (NIBRIV0000232657); and another 11 specimens (five males+three females+three copepodids) together in 99% ethanol, sample No. 12 (NIBRIV0000232657); South Korea, Gangwondo region, Pyeogchang city, Daehwa town, Daehwa stream, interstitial from beaches on banks, 37° 29'17"N 128° 27'23"E, 18 May 2010, leg. J.-L. Cho.

REMARKS: This species is unquestionably very closely related to the Japanese *P. biwae*, in so much so that they form a sister species pair. Both are also closely related to the widely distributed P. brevipes, but can be distinguished by the very small and spiniform endopod of the third leg in male, more inwardly curved posterior part of the caudal rami, more pronounced dorsal ridge on the caudal rami and longer dorsal caudal seta, very large and bilobate anterior chitinous process on the fourth leg basis in male, as well as wide and long outer endopodal lobe on the male fourth leg. However, even after Karanovic and Lee (2012) excluded the Korean population from P. brevipes and reinstated P. biwae as a valid species, there is very little doubt that the widely distributed European/North American P. brevipes, as redefined by Reid (1995), represents a complex of several closely related species. This is quite obvious now from the variations in the shape and size of the chitinous processes on the fourth leg basis in male, variations in relative length and proportions of the male sixth leg armature, as well as variations in the size of the inner-distal chitinous process on the female fifth leg (as illustrated by Reid, 1998: Figs. 3, 4), but will need further investigation to be properly solved. We especially refer here to the necessity for use of microcharacters (morphological characters associated with fine ornamentation of somites and appendages) and molecular characters. Combined morphological and molecular studies have shown recently a potential for short range endemism in this group of subterranean harpacticoids, with very little interspecific variability (Karanovic and Cooper, 2011a).

Differences between *P. koreana* and *P. biwae* are relatively settled but numerous, and many of them are arrowed in Figs. 59, 60. *Parastenocaris koreana* is a much smaller species (note that Figs. 35A, 59A are drawn to the same scale), with shorter caudal rami (proportionately to the anal somite), differently shaped anal operculum (concave versus convex), more elongated genital double somite in female, shorter inner distal process on the female sixth leg, as well as proportionately shorter apical setae of the second, third, and fourth legs exopods in both sexes.

Detailed examinations of the three disjunct populations of *P. koreana* revealed also some geographical variation, especially in the surface ornamentation of somites (i.e. smoothness and presence and frequency of cuticular pits (see Figs. 53–59)), which may indicate some population structuring (for example indicative of different subspecies) or even cryptic speciation. However, despite detailed analyses we were not able to find any additional and reliable morphological differences between these three populations. Similarly disjunct localities in Korea produced three short range endemics in the genus *Proserpinicaris* (see above), but with significant and reliable morphological differences between species. This would either suggest a different age for colonization of subterranean habitats for these two genera in Korea, or different evolutionary rates (as one can judge from their morphology anyway). Unfortuately, all Korean samples were preserved and stored in ethanol of less than 80%,

and our attempts to PCR amplify the COI gene have all failed. Remarkable similarities between our drawings and those of Lee and Chang (2009) (repeated in Chang, 2009, 2010), down to minute details in proportions of armature elements on the female swimming legs, are additional indication that we are dealing with a morphologically conservative population in Korea.

36. Parastenocaris lanceolata Enckell, 1970 (Fig. 61)

Parastenocaris lanceolata Enckell, 1970, p. 552, figs. 35-41.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 340 μ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of anal somite and caudal rami (Fig. 61A, B), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented with sensilla, pores, and spinules at least on some somites (no cuticular pits). Presumably preanal somite and three somites anterior to it with large, oval dorsal cuticular windows. Anal somite (Fig. 61A, B) ornamented only with pair of dorsal sensilla at base of anal operculum. Anal operculum (Fig. 61A, B) well developed, unornamented on outer surface, with slightly convex caudal margin, reaching posterior end of anal somite, and representing 61% of somite width. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 61A, B) about three times as long as greatest width (dorsal view) and almost 0.9 times as long as anal somite, conical, divergent, with space between them about 1.5 times one ramus width, armed with six armature elements (two lateral, one dorsal, and three apical), ornamented with two spinules along distal margin ventrally. Dorsal seta slender and smooth, inserted at mid-length of ramus and much closer to its inner margin, about 0.7 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted very close to each other, also at midlength. Proximal lateral seta inserted more dorsally, about three times as long as distal minute one, and about 0.8 times as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, slightly shorter than ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta smaller than middle apical seta but also relatively strong, also without breaking plane, smooth, about 1.2 times as long as ramus.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped unknown, but presumably similar to those in type species.

First swimming leg without armature on basis.

Second swimming leg (Fig. 61C) composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and three elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with straight inner margin, 2.4 times as long as greatest width, 1.8 times as long as endopod, with curved outer distal spine, slightly longer than segment. Endopod cylindrical and relatively slender, about 4.5 times as long as wide, reaching middle of first exopodal segment in length, ornamented with four large spinules along distal margin; armed apically with one smooth, slender inwards-pointing seta, about 0.8 times as long as segment.



Fig. 61. *Parastenocaris lanceolata*, Male. A. last two abdominal somites and caudal rami, dorsal view; B. last two abdominal somites and left caudal ramus, lateral view; C. basis, endopod, and first exopodal segment of second leg; D. third leg; E and F. basis, endopod, and first exopodal segment of fourth leg of two different specimens; G. fifth leg. Scales: 50 μ m (cited from Enckell, 1970, modified).

Third swimming leg (Fig. 61D) with coxa unornamented and fused to basis. Basis robust, trapezoidal in shape, armed with large outer smooth seta, ornamented with eight long spinules on outer margin (inner margin smooth). Endopod absent. Exopod with both segments fused; ancestral proximal segment about 2.9 times as long as wide, with slightly concave inner margin, with two outer cuticular protrusions on outer margin distally, ornamented with few spinules along outer margin distally, armed subapically with simple, strong, smooth and curved spine, 0.6 times as long as apophysis; ancestral distal segment (apophysis) cylindrical, oriented inwards, unornamented but with minute spiniform process apically, fused to segment; complex tridimensional structure of apophysis ends with membraneous bulbous part.

Fourth swimming leg (Fig. 61E, F) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process slightly longer but less strongly sclerotised, smooth and curved apically, simple structure, parallel to endopod; outer process somewhat shorter but much broader and more strongly sclerotised, pointing outward, simple structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, 3.3 times as long as greatest width, with slender outer distal spine, half as long as segment. Endopod one-segmented, very inflated proximally from anterior view, slightly longer than first exopodal segment, pointing inwards, armed with single smooth seta apically (broadly fused basally to segment), unornamented. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 61G) simple rectangular cuticular plate, inner distal margin unornamented and not produced posteriorly, ornamented with small spinule (or minute seta?) posterior to basal seta, armed with three smooth setae; outermost (ancestral basal) seta 2.5 times as long as middle seta and 1.7 times as long as innermost seta (middle and innermost setae probably ancestral endopodal armature).

Sixth legs unknown, probably very similar to type species.

Female: unknown.DL

TYPE: Type material lost.

TYPE LOCALITY: Sri Lanka, Sabaragamuwa Province, Bopathella Falls, 14.5 km east of Ratnapura, interstitial on banks of a small river.

DISTRIBUTION: The species is known from the type locality and an additional locality in the immediate vicinity, both near Ratnapura in Sabaragamuwa Province, Sri Lanka.

ECOLOGY: This species was recorded in small numbers at both localities (one male in each), which suggests that its prime habitat was probably not sampled. In both localities, *P. lanceolata* lives sympatrically with *P. noodti*, and in the second they live together with two more closely related congeners: *P. brincki* and *P. singhalensis*.

REMARKS: Enckell (1970) gave the body length of the holotype of *P. lanceolata* as 340 μ m. He, however, gave the same length for three other species from Sri Lanka, two of which live sympatrically with *P. lanceolata*. This makes it difficult to believe that he actually measured all specimens, because very often when closely related copepods live together they tend to differ significantly in size (Karanovic, 2006; Karanovic and Cooper, 2012). Unfortunately, he gave no habitus photos or illustrations and the type material is lost, which makes it impossible to check the actual sizes. The original description of this species is also incomplete; the shape of the fourth leg basis and endopod suggests that it belongs to the *brevipes* group of Lang (1948), which was recognised by Enckell (1970).

He, however, did not comment on the affinities of his new species, although the description was comparative to that of four closely related species (two of them sympatric; see above). He did note some variability in the shape of the fourth leg endoped between the two males examined.

The fifth leg of *P. lanceolata* is similar to that of *P. singhalensis*, i.e., without an inner distal spiniform process and with a smooth inner margin. The two species, however, differ significantly in the shape and ornamentation of their third and fourth legs. The shape of the male fourth leg seems to be most similar to that of *P. brincki*, although the latter has an additional row of spinules on the basis, and can be easily distinguished from *P. lanceolata* by the shape of its fifth and third legs. The most similar third leg to that of *P. lanceolata* is probably that of *P. noodti*, but the latter species differs from the former by its ornamented anal somite, as well as some additional ornamentation on the fourth and fifth legs.

37. Parastenocaris longipoda Shen and Tai, 1973 (Fig. 62)

Parastenocaris longipoda Shen and Tai, 1973, p. 380, figs. 96-107; Shen et al., 1979, p. 296, figs. 166, 167.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 460 to 530 μ m. Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 62A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width difficult to establish, probably at posterior end of cephalothorax. Body length/width ratio about 9.8; cephalothorax 1.2 times as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, without surface ornamentation reported (except normal sensilla and pores, but no spinules), cuticular windows probably not present. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, not reaching distal margin of first antennular segment.

Cephalothorax (Fig. 62A) about 1.8 times as long as wide in dorsal view; representing 18% of total body length. Ornamentation of surface of cephalic shield with sensilla unknown, as well as those of other somites.

Anal somite (Fig. 62A) probably ornamented with pair of large dorsal sensilla at base of anal operculum, 1.4 times as long as wide and 1.25 times as long as preanal somite. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing more than 70% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 62A) about three times as long as greatest width (dorsal view) and almost 0.6 times as long as anal somite, cylindrical (slightly narrowing towards distal end), unornamented, divergent, with space between them about 1.5 times one ramus width; armed with at least five armature elements (one lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/5 of ramus length, about as long as caudal ramus width, probably triarticulate basally. Lateral setae thin and smooth, inserted also at 3/5 of ramus length. Middle apical seta strongest, without breaking plane, smooth, about six times as long as outer

apical seta and 0.2 times as long as entire body. Outer apical seta also without breaking plane and smooth, relatively strong basally, about half as long as ramus.

Antennula (Fig. 62A) relatively long, seven-segmented, prehensile and strongly digeniculate, unornamented. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as large and sharp spiniform process; another smaller spiniform process present on fourth segment basally. Slender aesthetasc on fourth segment reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to at least one seta. Setal formula (certainly incomplete): 0.2.0.4.0.0.5. All setae slender and smooth.

Antenna relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 2.7 times as long as wide, unarmed, ornamented with short row of spinules on anterior surface. Endopod about 0.7 times as long as allobasis and 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, unornamented but armed with single unipinnate apical seta.

Mouth appendages unknown, but probably similar to those in type species.

First swimming leg with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with row of small spinules on outer margin (basal spine probably broken during dissection). Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine.

Second swimming leg with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with few spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and probably with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae). Endopod one-segmented, cylindrical and relatively short, about four times as long as wide, reaching midlength of first exopodal segment, ornamented with one large spinule on apical margin; armed apically with one smooth seta, about 1.2 times as long as segment.

Third swimming leg (Fig. 62B) with smooth praecoxa, coxa, and intercoxal sclerite, all fused with robust basis. Basis unornamented, armed with long outer seta. Endopod reduced to small seta or spine. Exopod well developed, prehensile, with both segments unarmed and unornamented; proximal segment three times as long as wide, almost cylindrical; distal segment conical, half as long as proximal segment, pointing inwards.

Fourth swimming leg (Fig. 62C) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into large processes. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta. Endopod one-segmented but somewhat constricted at midlength, half as long as first exopodal segment, two long spinules



Fig. 62. *Parastenocaris longipoda*. Male: A. habitus, dorsal view; B. third swimming leg; C. fourth swimming leg; D. fifth leg. Female: E. habitus, dorsal view; F. antennula; G. antenna; H. first swimming leg; I. second swimming leg; J. third swimming leg; K. fourth swimming leg; L. fifth leg. Scales: unknown (cited from Shen and Tai, 1973, modified).

apically.

Fifth leg (Fig. 62D) simple pentagonal cuticular plate, unornamented, armed with three smooth setae; outermost seta (ancestral basal one) longest, 3.6 times as long as entire leg, 1.5 times as long as middle seta and twice as long as inner seta.

Sixth legs unknown, but probably similar to those in type species.

Female: Body length, excluding caudal setae, from 460 to 530 μ m. Habitus (Fig. 62E) less slender than in male, only seven times as long as wide. Ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite.

Genital double somite (Fig. 62E) about as long as wide (dorsal view), without trace of subdivision or cuticular windows. Structure of genital complex unknown.

Caudal rami (Fig. 62E) similar to male but longer in proportion to anal somite and more divergent; armature same as in male.

Antennula (Fig. 62F) also seven-segmented, unornamented, with slender and short aesthetasc on fourth segment, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; setal formula (probably not complete): 0.3.1.2.1.1.5. All setae smooth.

Antenna (Fig. 62G), mandibula, maxillula, maxilla, maxilliped, first swimming leg (Fig. 62H), second swimming leg (Fig. 62I), and exopod of fourth swimming leg (Fig. 62K) similar to male.

Third swimming leg (Fig. 62J) with several spinules on coxa, near outer margin. Basis ornamented with three spinules on outer margin distally, armed with very long and finely pinnulate outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, straight, unornamented, armed with apical strong spine, fused basally to segment, reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 62K) without spiniform processes on basis. Endopod one-segmented but very large, about as long as exopod, ornamented with single spinule on inner margin and about 2/5 of its length, which probably indicates ancestral articulation of apical spine. Exopod similar to male, but with inner margin less concave.

Fifth leg (Fig. 62L) also simple cuticular plate, but much larger than in male and with inner distal corner produced into long and spiniform process, about as long as rest of leg. Armature and ornamentation same as in male.

Sixth legs unknown but probably similar to those in type species.

TYPE: All material deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

TYPE LOCALITY: China, Guangxi Province, Pingguo County, Xi Jiang (= West River).

DISTRIBUTION: This species was collected from two localities on Xi Jiang (= West River), Guiping City and Pingguo County, both in Guangxi Province, China.

ECOLOGY: Nothing is known about its ecology.

REMARKS: The extremely long endopod of the fourth leg in female (Fig. 62K) distinguishes this species from any other known parastenocarid, except perhaps from some specimens of *Parastenocaris brevipes*. However, the two differ in the shape of the fourth leg endopod in male, as well as the shape of the fifth legs in both sexes. The shape of the fifth leg in the female of *P. longipoda*, with its long and wide inner distal process, is also very characteristic.

38. Parastenocaris muvattupuzha Ranga Reddy and Defaye, 2009 (Fig. 63)

Parastenocaris muvattupuzha Ranga Reddy and Defaye, 2009, p. 32, figs. 2-8.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 365 to 410 μ m (395 μ m in allotype). Preserved specimen colourless. Nauplius eve absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 63A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.8; greatest width difficult to establish. Body length/width ratio about 7.3; cephalothorax 1.1 times as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all prosomites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Hyaline fringes of urosomites serrated dorsally. Integument relatively weakly sclerotised, very smooth, ornamented with sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on genital and three postgenital somites (Fig. 63A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax very similar to that in female (Fig. 63I), about 1.5 times as long as wide in dorsal view; representing 20% of total body length. Ornamentation of surface of cephalic shield with sensilla dorsally relatively simple: six sensilla around double cuticular window, one additional pair posteriorly, one pair at middle between double window and rostrum, one pair more ventrally at about same level, and two pairs anteriorly.

Urosomal somites (except preanal somite, unornamented) with six posterior sensilla and with serrated hyaline fringe dorsally and sometimes laterally.

Anal somite (Fig. 63A) ornamented with lateral pore anteriorly and pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with strongly concave and smooth distal margin, not reaching posterior end of anal somite, representing 68% of somite width. Anal sinus widely opened, ornamented with several rows of slender spinules.

Caudal rami (Fig. 63A, B) about 3.7 times as long as greatest width (dorsal view) and almost 0.8 times as long as anal somite, cylindrical (slightly narrowing towards distal end), slightly divergent, with space between them about 1.5 times one ramus width, with inner distal corner produced into small dentate process; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of several small spinules along posterior margin ventrally. Dorsal seta slender and smooth, inserted closer to inner margin at about midlength, slightly longer than caudal ramus, triarticulate basally. Lateral setae thin and smooth, inserted close to each other, also around midlength. Proximalmost lateral seta placed more dorsally, 0.4 times as long as ramus, about 1.5 times as long as middle seta, and 2.5 times as long as distalmost (ventralmost) minute seta. Inner apical seta small, smooth, inserted more ventrally, about 0.6 times as long as ramus. Middle apical seta strongest, without breaking plane, unipinnate, about 3.9 times as long as outer apical seta and almost 0.27 times as long as whole body. Outer apical seta also without breaking plane and unipinnate, relatively strong basally, about 1.2 times as long as ramus.

Antennula relatively long, seven-segmented, prehensile and digeniculate, ornamented with ventral



Fig. 63. *Parastenocaris muvattupuzha*. Male: A. urosome, lateral view; B. left caudal ramus, lateral view; C. first swimming leg with only first exopodal and endopodal segments; D. third swimming leg, anterior view; E. fourth swimming leg without last two exopodal segments, anterior view. F. endopod of fourth swimming leg and two basal processes; G. fifth leg, anterior view. Female: H. habitus, dorsal view; I. cephalothorax, dorsal view; J. anal somite and caudal rami, dorsal view; K. first swimming leg, anterior view; L. second swimming leg, anterior view; M. third leg, anterior view; N. fourth leg without last two endopodal segments, anterior view; O. fifth leg, anterior view. Scales: 50 μ m (cited from Ranga Reddy and Defaye, 2009, modified).

row of spinules on first segment. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as spiniform process; another spiniform process present on fourth segment basally. Slender aesthetasc on fourth segment reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula: 0.7.4.2.0.0.8. All setae slender and all except largest seta on second segment smooth.

Antenna relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and onesegmented exopod. Coxa very short, unornamented. Allobasis about 3.7 times as long as wide, unarmed, ornamented with two short rows of minute spinules on anterior surface. Endopod about 0.6 times as long as allobasis and 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about 2.3 times as long as wide, unornamented but armed with single unipinnate apical seta, twice as long as segment.

Mandibula with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula with relatively small praecoxa, arthrite rectangular, about 1.4 times as long as wide in lateral view, unornamented but armed with strong lateral seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two smooth apical setae. Endopod and exopod absent (fused to basis without trace).

Maxilla unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, basal armed with single smooth seta apically, distal armed with one smooth and one pinnate seta apically. Basis drawn out into strong and smooth claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped with very short syncoxa, unarmed and unornamented; basis slender, about five times as long as wide and as many times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.7 times as long as basis.

First swimming leg (Fig. 63C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with bunch of large spinules on outer margin, and another on posterior margbetween exopod and endopod, armed with single short seta on outer margin and another slender but longer seta on inner margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.5 times as long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, about six times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along apical margin; armed apically with one smooth seta, about 0.7 times as long as segment and pointing inwards.

Third swimming leg (Fig. 63D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod a minute but distinct segment, about half as long as largest spinule on outer margin and only slightly stronger, unornamented and armed apically with smooth seta basally fused to segment. Exopod with both segments fused; ancestral proximal segment twice as long as wide, curved inwards and gently tapering towards distal end, with large chitinous beak on inner margin distally, unornamented, armed subapically with simple, strong, smooth and curved spine, somewhat shorter than apophysis; ancestral distal segment (apophysis) conical, oriented inwards, unornamented and unarmed, with small chitinous beak on inner margin distally.

Fourth swimming leg (Fig. 63E, F) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into two processes; inner process narrow and less strongly sclerotised, smooth and pointing slightly inwards; outer process much broader and more strongly sclerotised, with serrate distal margin, pointing outwards, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta nearly as long as entire exopod and more than twice as long as outer spine. Endopod one-segmented, club-shaped, distally with brush of spinules on medial surface.

Fifth leg (Fig. 63G) simple triangular cuticular plate, inner distal corner produced into short and smooth spiniform process, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, 1.8 times as long as entire leg; next seta (probably ancestral exopodal) very small and spiniform, almost resembling spinule; third seta from outer side (ancestral outer endopodal) slightly shorter than leg, and 1.4 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 335 to 425 μ m (405 μ m in holotype). Habitus (Fig. 63H), ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite, and habitus slightly less slender.

Genital double somite (Fig. 63H) slightly longer than wide (dorsal view), without trace of subdivision, with large oval dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami (Fig. 63J) similar to male but slightly shorter in proportion to anal somite and with somewhat shorter inner apical seta.

Antennula also seven-segmented, unornamented, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused

basally to two apical setae; both aesthetascs equally slender as in male; setal formula: 0.4.4.2.1.0.8. All setae, except proximalmost one on second segment, smooth.

Antenna, mandibula, maxillula, maxilla, maxilliped, second swimming leg (Fig. 63L), and exopod of fourth swimming leg (Fig. 63N) similar to male.

First swimming leg (Fig. 15K) without inner seta on basis, but otherwise same as in male.

Third swimming leg (Fig. 63M) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with several spinules on outer margin distally, armed with very long and smooth outer seta, slightly longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and strong apical seta; all elements bipinnate. Endopod one-segmented, small, straight, unornamented, armed with apical strong spine, fused basally to segment, not reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 63N) without spiniform processes on basis. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, not distinct at base, bipinnate, and about as long as endopod; endopod with apical spine reaching slightly beyond posterior margin of first exopodal segment in length. Exopod similar to male, but with inner margin less concave.

Fifth leg (Fig. 42S) also simple cuticular plate, but with inner distal corner produced into long and spiniform process. Armature and ornamentation same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed.

TYPE: Type material deposited in the National Museum of Natural History, Paris.

TYPE LOCALITY: India, Kerala, River Muwattupuzha at Muwattupuzha Town, hyporheic sediment to a depth of 10–30 cm.

DISTRIBUTION: This species is known only from the type locality, River Muwattupuzha in India.

ECOLOGY: Specimens were obtained from core samples taken from a hyporheic habitat, from the sediment surface to a depth of 10–30 cm. The maximum length of the river is about 120 km, and the drainage area is rich in crystalline rocks of igneous and metamorphic origin. The riverbed at the sampling site had a deposit of fine sand and detritus particles, but with little or no clay, and was devoid of macrophytic vegetation. The species was found sympatrically with *Parastenocaris curvispinus* Enckell, 1970, as well as with nematodes, oligochaetes, insect larvae, and a parabathynellid from the genus *Habrobathynella* Schminke, 1973.

REMARKS: The unusual club-shaped structure of the fourth leg endopod in the male, makes it very difficult to include this species in the *brevipes* group, despite the two characteristic chitinous processes of the basis. Ranga Reddy and Defaye (2009) opted not to include their new species in this group, also based on the lack of sexual dimorphism in the swimming legs. Schminke (2010) argued that the species is the newest addition to the *brevipes* group (and his *Parastenocaris s. str.*), but did not provide any argument for this decision, nor did he question Ranga Reddy and Defaye's (2009) reasoning. We agree with Schminke (2010), as the lack of sexual dimorphism in the fifth legs is probably a plesiomorphic character, and the paired chitinous processes on the fourth leg basis are unusual and rare structures in copepod crustaceans, and the chances of their independent origin in unrelated taxa are probably very small. Ranga Reddy and Defaye (2009) stated that *P. muwattupuzha* differs from all other parastenocaridids by the unguiform process at the inner distal corner of the caudal ramus, but a similar structure was also observed and nicely photographed in *Parastenocaris pasquinii* Bruno and Cottarelli, 1998 (see Figs. 10E, 11A in Bruno and Cottarelli, 1998).

39. Parastenocaris noodti Enckell, 1970 (Fig. 64)

Parastenocaris noodti Enckell, 1970, p. 548, figs. 16-26.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 340 μ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of anal somite and caudal rami (Fig. 64A, B), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites smooth, very narrow, and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented with sensilla, pores, and spinules at least on some somites (no cuticular pits). Presumably preanal somite and three somites anterior to it with large, oval dorsal cuticular windows. Anal somite (Fig. 64A) ornamented with pair of dorsal sensilla at base of anal operculum, as well as with two arched rows of large sensilla dorsally. Anal operculum (Fig. 64A, B) well developed, unornamented on outer surface, with convex caudal margin, almost reaching posterior end of anal somite, and representing 53% of somite width. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 64A, B) about 2.5 times as long as greatest width (dorsal view) and almost 0.7 times as long as anal somite, conical, slightly divergent, with space between them about 1.5 times one ramus width, armed with six armature elements (two lateral, one dorsal, and three apical), ornamented with two spinules at base of lateral setae, several spinules on outer margin distally, and transverse row of spinules along distal margin ventrally. Dorsal seta slender and smooth, inserted at 3/5 of ramus length and somewhat closer to inner margin, about as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other, at 3/5 of ramus length. Proximal lateral seta inserted more dorsally, about 2.3 times as long as distal minute one, and about 0.6 times as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, slightly shorter than ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta smaller than middle apical seta but also relatively strong, also without breaking plane, smooth, about 1.4 times as long as ramus.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown, but presumably similar to those in type species.

Second swimming leg (Fig. 64C) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and three elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, 2.8 times as long as greatest width, 2.2 times as long as endopod, with curved outer distal spine, significantly longer than segment. Endopod cylindrical and relatively slender, about 3.8 times as long as wide, not reaching middle of first exopodal segment in length, ornamented with four large spinules along distal margin; armed apically with one smooth, inwards-pointing slender seta, about 0.8 times as long as segment.

Third swimming leg (Fig. 64D) with coxa ornamented with short row of spinules. Basis robust, trapezoidal, unarmed, ornamented with eight long spinules on outer margin (inner margin smooth). Endopod absent. Exopod with both segments fused; ancestral proximal segment about 2.5 times as long as wide, with concave inner margin, ornamented with few spinules along outer margin distally, armed subapically with simple, strong, smooth and curved spine, 0.7 times as long as apophysis; ancestral distal segment (apophysis) cylindrical, oriented inward, unornamented but with minute



Fig. 64. *Parastenocaris noodti*. Male: A. last two abdominal somites and caudal rami, dorsal view; B. last two abdominal somites and left caudal ramus, lateral view; C. basis, endopod, and first exopodal segment of second leg; D. third leg; E. basis, endopod, and first exopodal segment of fourth leg, inner view; G. fifth leg. Female: H. basis, endopod and first exopodal segment of second leg; I. basis, endopod, and first exopodal segment of third leg; J. basis, endopod, and first exopodal segment of third leg; J. basis, endopod, and first exopodal segment of third leg; J. basis, endopod, and first exopodal segment of third leg; J. basis, endopod, and first exopodal segment of fourth leg; K. fifth leg. Scales: 50 μ m (cited from Enckell, 1970, modified)

spiniform process apically, fused to segment; complex tridimensional structure of apophysis ends with membraneous bulbous part.

Fourth swimming leg (Fig. 64E, F) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process slightly longer but less strongly sclerotised, smooth and curved apically, simple structure, parallel to endopod; outer process somewhat smaller, but more strongly sclerotised, pointing outward, simple structure, not reaching outer margin of endopod, and shielding proximal part of endopod. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, three times as long as greatest width, with stout outer distal spine, 0.7 times as long as segment. Endopod one-segmented, very inflated from anterior (or posterior) view, but less so from lateral view (Fig. 64F), slightly longer than first exopodal segment, and parallel with it, armed with single smooth seta apically (broadly fused basally to segment), ornamented with longitudinal row of small spinules both on anterior and posterior surface. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 44F) simple trapezoidal cuticular plate, inner distal margin produced posteriorly only slightly, ornamented with small spiniform process posterior to basal seta (this probably fused spinules) and three spinules along inner margin distally, armed with three smooth setae of about same length.

Sixth legs unknown, probably very similar to type species.

Female: Body length same as in male, and presumably also habitus shape, ornamentation of somites, colour, and nauplius eye.

Genital double somite unknown. Anal somite and caudal rami same as in male. Antennula unknown, probably similar to type species. Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg probably similar to male.

Second swimming leg (Fig. 64H) also very similar to male, but first exopodal segment with inner margin slightly more concave; endopod proportionately longer.

Third swimming leg (Fig. 64I) composed of praecoxa, coxa, intercoxal sclerite, basis, two-segmented exopod, and one-segmented endopod. First exopodal segment rectangular, 2.7 times as long as wide, ornamented with several large spinules on outer margin, few spinules on outer distal corner, and hyaline frill distally on inner side; armed with stout and smooth outer spine, about 0.8 times as long as first exopodal segment. Endopod small and simple, fused basally to apical smooth spine, half as long as first exopodal segment, straight.

Fourth swimming leg (Fig. 64) without spiniform processes on basis. Endopod one-segmented, slender, curved slightly inwards, ornamented with several spinules at base of apical spine, not completely distinct at base, bipinnate, and about as long as endopod. Endopod with its apical spine about 1.4 times as long as first exopodal segment. Exopod similar to male, but first segment with less-concave inner margin, longer outer spine, and more spinules on outer margin.

Fifth leg (Fig. 64K) similar to male, but more elongated, and with inner distal corner produced into relatively short spiniform process; outer basal seta shorter (but possibly broken); outer endopodal seta 1.8 times as long as inner endopodal seta (these two of similar length in male).

Sixth legs unknown but probably vestigial, fused into simple cuticular plate, covering gonopore; ornamentation and armature unknown.

TYPE: Type material lost.

TYPE LOCALITY: Sri Lanka, Sabaragamuwa Province, Bopathella Falls, 14.5 km east of Ratnapura, interstitial on banks of a small river.

DISTRIBUTION: Known from the type locality and one more locality in the immediate vicinity, both near Ratnapura in Sabaragamuwa Province, Sri Lanka.

ECOLOGY: This is also an interstitial species, but with preferences for coarse gravel. In the type locality it was collected together with one other congener, but in the second locality it lives sympatrically with three other species of *Parastenocaris*, two of which are also from the *brevipes* group.

REMARKS: Although the original description of this species is incomplete, the shape of the fourth leg basis and endopod would suggest it belongs to the *brevipes* group of Lang (1948), which was recognised by Enckell (1970). He, however, did not comment on the affinities of his new species, although the description was comparative to that of a closely related (but not sympatric) *P. irenae* (see above). The two species differ by a number of characters, the most prominent ones being the ornamentation of the anal somite and shape of the male fifth leg. In fact, *P. noodti* is the only Sri Lankan species with large dorsal spinules on the anal somite.

40. Parastenocaris oshimaensis Miura, 1962 (Fig. 65)

Parastenocaris oshimaensis Miura, 1962, p. 102, figs. 40-49.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), 430 μ m. Preserved specimen white. Nauplius eye absent. Body cylindrical, vermiform, composed of prosome (consisting of cephalothorax and three free pedigerous somites of which the first pedigerous somite is fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Hyaline fringes of somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented with sensilla and pores at least on some somites (no cuticular pits or spinules). Information on cuticular windows not available. Anal somite (Fig. 65A) probably ornamented only with pair of dorsal sensilla at base of anal operculum. Anal operculum well developed, with slightly convex caudal margin, unornamented on outer surface but with row of very small spinules on distal margin (probably on ventral surface), not reaching posterior end of anal somite. Anal sinus widely opened, probably also ornamented with spinules.

Caudal rami (Fig. 65A) about 3.3 times as long as greatest width (ventral view), cylindrical in anterior part but conical in posterior part, divergent, with space between them nearly twice one ramus width, armed with at least five armature elements (two lateral, one dorsal, and two apical), ornamented with semi-crescentic row of spinules on dorsal surface posteriorly. Dorsal seta slender and smooth, inserted at 3/5 of ramus length and much closer to its inner margin, about half as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted also at 3/5 of ramus length and slightly more ventrally; proximal seta about 0.3 times as long as ramus and twice as long as distal seta. Inner apical seta probably reduced or very small and not observed. Principal apical seta strongest, without breaking plane, length unknown. Outer apical seta much smaller than principal apical seta but also relatively strong and without breaking plane, smooth, about 0.7 times as long as ramus.

Ornamentation of somites, rostrum, labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped unknown, but presumably similar to those in type species.
Antennula probably seven-segmented, prehensile, with large aesthetasc on fourth segment. Antenna as in type species. Endopod one-segmented, armed with single apical seta.

First swimming leg composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and two-segmented endopod. First exopodal segment ornamented with two groups of spinules on outer margin; second segment with two slender spinules on outer margin; third segment with spinules on outer margin and armed as in other species with four elements. Endopod two-segmented, about as long as exopod; first segment unarmed but ornamented with two groups of slender spinules on outer margin; second segment armed with two elements.

Second swimming leg (Fig. 65B) composed of praecoxa, coxa (partly fused to praecoxa), intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod. Exopod ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one slightly longer than exopod; all exopodal armature pinnate. Endopod cylindrical and relatively slender, about 3.6 times as long as wide, reaching middle of first exopodal segment in length, ornamented with three large spinules along distal margin; armed apically with one smooth, slender, inwards-pointing seta, about 0.7 times as long as segment.

Third swimming leg (Fig. 65C) with praecoxa and coxa unornamented and relatively small. Basis robust, rectangular, armed with large outer smooth seta, ornamented with 14 long spinules on anterior surface diagonally from base of outer seta to distal inner corner. Endopod absent. Exopod with both segments fused; ancestral proximal segment about 2.4 times as long as wide, curved inwards and slowly tapering towards distal end, with slightly concave inner margin, and with what seems like shallow depression on anterior surface, unornamented, armed subapically with simple, strong, smooth and curved spine, 0.6 times as long as apophysis; ancestral distal segment (apophysis) conical, oriented inwards, unornamented, simple structure.

Fourth swimming leg (Fig. 65D) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process shorter and less strongly sclerotised, smooth and parallel to endopod; outer process much broader and more strongly sclerotised, pointing outward, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, almost straight, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with slightly concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and long and strong apical seta; apical seta 0.9 times as long as entire exopod and 2.3 times as long as outer spine. Endopod one-segmented, not curved inwards, conical structure in anterior view, with inflated proximal part, slightly shorter than first exopodal segment, unornamented and unarmed. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 65E) simple rhomboidal cuticular plate, inner distal margin unornamented and only slightly produced posteriorly, unornamented, armed with four smooth setae; outermost (ancestral basal) seta nearly eight times as long as other three setae, which are subequal.

Sixth legs unknown, probably very similar to type species.

Female: Body length, excluding caudal setae, 400 μ m. Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite (Fig. 65G).

Genital double somite (Fig. 43G) about as long as wide without trace of subdivision; ornamentation unknown; genital complex occupying anterior ventral half of genital double somite; genital apertures



Fig. 65. *Parastenocaris oshimaensis*. Male: A. last two urosomal somites and caudal rami, dorsal view; B. second swimming leg; C. third swimming leg, anterior view; D. fourth swimming leg, anterior view; E. fifth leg, anterior view. Female: F. last two urosomal somites and caudal rami, ventral view; G. fifth pedigerous somite with fifth legs and anterior half of genital double somite, ventral view; H. second swimming leg; anterior view; I. third swimming leg, anterior view; J. fourth swimming leg, anterior view. Scale unknown (cited from Miura, 1962, modified).

closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory ducts very short and weakly sclerotised. Anal somite very similar to male. Anal operculum (Fig. 65F) with almost straight caudal margin.

Caudal rami (Fig. 65F) similar to male but slightly shorter in proportion to anal somite and slightly wider at middle from ventral view, about 2.6 times as long as wide (ventral view); ornamentation and armature same as in male.

Antennula seven-segmented, with slender aesthetasc also on fourth segment. Antenna, mandibula, maxillula, maxilla, and maxilliped unknown but probably similar to those of male. First swimming leg very similar to that of male.

Second swimming leg (Fig. 65H) similar to that of male, but with proportionately shorter armature on third exopodal segment and only one large spinule on endopod.

Third swimming leg (Fig. 65I) without clear demarcation between praecoxa and coxa, both also unornamented. Basis armed with very long and smooth outer seta, longer than first exopodal segment, ornamented with row of five small spinules on anterior surface close to outer margin. Exopod two-segmented, ornamented with few large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, parallel to exopod, conical, armed with single seta on top fused to segment basally, unornamented, 0.75 times as long as first exopodal segment.

Fourth swimming leg (Fig. 65J) without clear demarcation between praecoxa, coxa, and basis; all also unornamented; basis armed with slender and smooth outer seta. Endopod one-segmented, ornamented with single apical spinule at base of apical spine, distinct at base, unipinnate, and slightly longer than endopod. Exopod similar to male, but with slightly more robust first segment.

Fifth leg (Fig. 65G) trapeziform, armed with four setae as in male, with inner distal corner produced into short spiniform process, and shorter outermost (ancestral basal) seta.

Sixth legs (Fig. 65G) vestigial, not fused medially, covering gonopores, unornamented and unarmed.

TYPE: Type material probably lost.

TYPE LOCALITY: Japan, China Prefecture, Ryukyu Islands, Okinerabu Island, Shinjo, Fuki-go Cave. **DISTRIBUTION:** This species is only known from the type locality, Fuki-go Cave, on Okinoerabu Island, Amami group of Ryukyu Islands, Japan.

ECOLOGY: The precise environment of this species in the cave is unknown, but at the time of collection the water temperature was 21.5°C and the pH was 8. The cave is formed in coral limestone, probably of relatively recent origin (Miura, 1962), but the rich freshwater fauna is probably a result of repeated separation and reattachment to the Eurasian continent.

REMARKS: Miura (1962) remarked that *P. oshimensis* is probably most closely related to *P. feuerborni* from Sumatra but it differs by the ornamentation of the anal operculum, as well as the shape and ornamentation of the third, fourth, and fifth legs in male. We should point out that Miura (1962) interpreted the spinules on the anal operculum as being on the dorsal surface, but they were probably originating from the ventral surface and only protruding lightly beyond the posterior margin. This situation is common in many species of the *brevipes* group, although the spinules can be more or less developed. In our view, a more important character is the semi-crescentic row of dorsal spinules on the caudal rami. The drawings of the fifth legs for both sexes are quite schematic and do not allow for confident comparison. It is remarkable if they really do not show any sexual dimorphism, but that would need to be checked on newly collected material.

41. Parastenocaris palmerae Reid, 1991 (Fig. 66)

Parastenocaris palmerae Reid, 1991, p. 2897, figs. 21-43.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 360 to 492 μ m (390 μ m in allotype). Preserved specimen pale grey. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 66A) cylindrical and very slender, without demarcation between prosome and urosome; greatest width difficult to establish. Free pedigerous somites without expansions laterally or dorsally, all connected by welldeveloped arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument relatively weakly sclerotised, very smooth, without surface ornamentation except sensilla and pores (no spinules), dorsally with round cuticular double window on cephalothorax and oval cuticular simple windows on genital and three postgenital somites (Fig. 66A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax about 1.5 times as long as wide in dorsal view; representing 19% of total body length. Ornamentation of surface of cephalic shield with sensilla unknown, as well as those of other somites, probably very similar to type species.

Anal somite (Fig. 66A) ornamented with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with convex and smooth distal margin, not reaching posterior end of anal somite, representing 65% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 66A) about 2.4 times as long as greatest width (dorsal view) and only half as long as anal somite, cylindrical (slightly narrowing towards distal end), slightly divergent, with space between them about 1.5 times one ramus width, unornamented; armed with seven armature elements (three lateral, one dorsal, and three apical). Dorsal seta slender and smooth, inserted closer to inner margin at about 3/4 of ramus length, about 0.6 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other, also at 3/4 of ramus length. Proximalmost lateral seta placed more dorsally, 0.4 times as long as ramus, about 1.5 times and long as middle seta, and twice as long as distalmost (ventralmost) minute seta. Inner apical seta long, smooth, inserted more ventrally, about 1.5 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 1.5 times as long as outer apical seta and almost three times as long as caudal ramus. Outer apical seta also without breaking plane and smooth, relatively strong basally, about twice as long as ramus.

Antennula (Fig. 66B) relatively long, seven-segmented, prehensile and strongly digeniculate, ornamented with few spinules on first segment. First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as small spiniform process; another small spiniform process present on fourth segment basally. Slender aesthetasc on fourth segment reaching tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula: 0.5.4.3.0.1.8. All setae slender and all except largest seta on second segment smooth.

Antenna, labrum, paragnaths, mandibula, maxillula, maxilla, and maxilliped unknown, but presumably similar to those in type species.

First swimming leg similar to that of female (Fig. 66J) with smooth praecoxa, coxa, and intercoxal



Fig. 66. *Parastenocaris palmerae*. Male: A. urosome, dorsal view; B. antennula; C. endopod of second swimming leg; D. third swimming leg, anterior view; E. fourth swimming leg, anterior view; F. fifth leg, anterior view. Female: G. habitus, dorsal view; H. right caudal ramus, lateral view; I. distal part of antennula; J. first swimming leg, anterior view; K. second swimming leg, anterior view; L. third swimming leg, anterior view; M. fourth swimming leg without last two exopodal segments, anterior view; N. fifth leg, anterior view. Scales: 100 μ m (cited from Reid, 1991, modified).

sclerite. Basis somewhat shorter than coxa, pentagonal, ornamented with row of small spinules on distal margin, additional row of larger spinules on outer margin, but unarmed. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.7 times as long as entire endopod and 1.8 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 66C) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with single outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae); all exopodal armature bipinnate. Endopod one-segmented, cylindrical and long, but slightly curved inwards, about four times as long as wide, reaching 3/4 of first exopodal segment in length, ornamented with three large spinules along apical margin; armed apically with one smooth seta, about as long as segment and pointing inwards.

Third swimming leg (Fig. 66D) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin, and longitudinal row of small spinules along inner margin. Endopod minute but distinct, seta-like, slightly larger than largest spinules on basis. Exopod with both segments fused; ancestral proximal segment more than four times as long as wide, curved inwards and slowly tapering towards distal end, with small chitinous beak on inner margin, ornamented with two short rows of large spinules on outer margin proximally, armed subapically with simple, strong, smooth and curved spine, about half as long as apophysis; ancestral distal segment (apophysis) spiniform, oriented inwards, unornamented, simple structure; exopodal spine and apophysis pointing at 90° angle.

Fourth swimming leg (Fig. 66E) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into two processes; inner process simple, narrow and less strongly sclerotised, smooth and nearly parallel to endopod (although tip pointing slightly outwards); outer process much broader and more strongly sclerotised, tricuspidate, pointing distally, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave inner margin in proximal half, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta about as long as entire exopod and almost three times as long as outer spine. Endopod one-segmented, armed apically with single unipinnate spine, slightly longer than first exopodal segment, unornamented.

Fifth leg (Fig. 66F) simple trapezoidal cuticular plate, with inner distal corner produced into short and smooth spiniform process, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, almost as long as entire leg; next seta (probably ancestral exopodal) very small and spiniform; third seta from outer side (ancestral outer endopodal) 0.6 times as long as leg, and 1.7 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming trapezoidal flap.

Female: Body length, excluding caudal setae, from 336 to 412 μ m (432 μ m in holotype). Habitus (Fig. 66G), ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somite fused into double somite, and habitus slightly less slender.

Genital double somite slightly wider than long (dorsal view), without trace of subdivision, with large saddle-like dorsal cuticular window in anterior half, much larger than that in male (originating from fused windows of two ancestral somites). Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male, but anal somite slightly shorter (Fig. 66G).

Caudal rami (Fig. 66G, H) similar to male but slightly larger in proportion to anal somite; armature similar to male, but outer apical seta proportionately shorter.

Antennula (Fig. 66I) also seven-segmented, unornamented, with slender aesthetasc on fourth segment, not reaching tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (probably not complete): 0.1.5.2.0.1.6. All setae smooth.

Antenna, mandibula, maxillula, maxilla, and maxilliped unknown but probably similar to male. First swimming leg (Fig. 66J), second swimming leg (Fig. 66K), and exopod of fourth swimming leg (Fig. 66M) similar to male.

Third swimming leg (Fig. 66L) with large praecoxa, smooth coxa, and intercoxal sclerite. Basis ornamented with three spinules on outer margin distally, armed with very long and smooth outer seta, slightly shorter than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second with outer spine and strong apical seta; all elements bipinnate. Endopod one-segmented, small, straight, unornamented, armed with strong apical spine, fused basally to segment, not reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 66M) without spiniform processes on basis, but with row of small spinules at base of endopod. Endopod one-segmented, ornamented with transverse apical row of three spinules at base of apical spine, distinct at base, bipinnate, straight, and about as long as endopod; endopod with apical spine reaching distal margin of first exopodal segment in length. Exopod similar to male, but with inner margin less concave.

Fifth leg (Fig. 66N) also simple cuticular plate, but with inner distal corner produced into longer spiniform process. Armature and ornamentation same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed.

TYPE: Type material in the US National Museum of Natural History, Smithsonian Institution, Washington.

TYPE LOCALITY: USA, northern Virginia, Loudoun County, Goose Creek, interstitial sediments in the stream bed.

DISTRIBUTION: This species is known only from the type locality, Goose Creek in the USA.

ECOLOGY: This is another interstitial species that lives in river beds.

REMARKS: This species differs from other members of the *brevipes* group by several characters: endopod of the fourth leg in male armed apically with spiniform spine; fifth leg in male with spiniform process present (although smaller than in female), and dorsal seta and all lateral setae on caudal rami situated more posteriorly. The first two characters are probably plesiomorphic in a larger group of species, while it is difficult to say whether the last one is plesiomorphic or apomorphic. All other

characters fit well with other members of the *brevipes* group, and Karanovic (2005a) argued that there is no reason to exclude it, as proposed by Reid (1995).

42. Parastenocaris savita Ranga Reddy, 2001 (Fig. 67)

Parastenocaris savita Ranga Reddy, 2001, p. 716, figs. 5-7.

Male: Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 420 to 480 μ m (470 μ m in holotype). Preserved specimen colourless. Nauplius eye absent. Body composed of prosome (consisting of cephalothorax and three free pedigerous somites, first pedigerous somite fused to cephalothorax), and urosome (consisting of fifth pedigerous somite, genital somite, four abdominal somites, and caudal rami). Habitus (Fig. 67A) cylindrical and very slender, without demarcation between prosome and urosome; prosome/urosome ratio 0.7; greatest width at posterior end of cephalothorax (dorsal view). Body length/width ratio about 8.9; cephalothorax 1.1 times as wide as genital somite. Free pedigerous somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of all somites smooth, very narrow and difficult to distinguish from arthrodial membranes, especially dorsally. Integument weakly sclerotised, very smooth, without surface ornamentation except sensilla and pores (no spinules), dorsally with round cuticular window on cephalothorax and oval cuticular windows on three postgenital somites (Fig. 67A). Pleural areas of cephalothorax and free pedigerous somites not well developed, cephalic appendages and coxae of swimming legs clearly exposed in lateral view. Rostrum small, membraneous, not demarcated at base, ornamented with two large dorsal sensilla, linguiform, almost reaching distal margin of first antennular segment, about twice as long as wide.

Cephalothorax (Fig. 67A) about 1.5 times as long as wide in dorsal view; representing 16 % of total body length. Ornamentation of surface of cephalic shield with sensilla unknown, as well as those of other somites.

Anal somite (Fig. 67B) probably ornamented with pair of large dorsal sensilla at base of anal operculum. Anal operculum well developed, unornamented on outer surface, with concave and smooth distal margin, reaching posterior end of anal somite, representing 59% of somite width. Anal sinus widely opened, unornamented.

Caudal rami (Fig. 67A, B) about 3.3 times as long as greatest width (dorsal view) and almost 0.7 times as long as anal somite, cylindrical (slightly narrowing towards distal end), divergent, with space between them about 1.5 times one ramus width; armed with seven armature elements (three lateral, one dorsal, and three apical). Ornamentation consists of large spinule ventrolaterally close to posterior margin. Dorsal seta slender and smooth, inserted closer to inner margin at about 3/5 of ramus length, about 0.7 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted close to each other also at 3/5 of ramus length. Proximalmost lateral seta placed more dorsally, 0.4 times as long as ramus, about 2.8 times and long as middle seta, and 5.2 times as long as distalmost (ventralmost) minute seta. Inner apical seta small, smooth, inserted more ventrally, about 0.7 times as long as ramus. Middle apical seta strongest, without breaking plane, smooth, about 3.4 times as long as outer apical seta and 0.3 times as long as entire body. Outer apical seta, also without breaking plane and smooth, relatively strong basally, about as long as ramus.

Antennula (Fig. 67C) relatively short, seven-segmented, prehensile and digeniculate, unornamented.

First segment very short, second segment longest. Geniculation between third and fourth and between fifth and sixth segments. Distal anterior corner of sixth segment protrudes as large spiniform process; another spiniform process present on fourth segment basally. Slender aesthetasc on fourth segment reaching beyond tip of appendage, fused basally to slightly longer seta. Much shorter apical aesthetasc on seventh segment, fused basally to two setae. Setal formula (probably incomplete): 0.5.2.1.0.0.7. All setae slender, and all except largest seta on second segment smooth.

Antenna (Fig. 67D) relatively stout and long, composed of coxa, allobasis, one-segmented endopod, and one-segmented exopod. Coxa very short, unornamented. Allobasis about 3.4 times as long as wide, unarmed, ornamented with two short spinules along anterior surface. Endopod about 0.6 times as long as allobasis and 2.3 times as long as wide, with surface frill subdistally, ornamented with few large spinules along anterior surface, armed laterally with two bipinnate spines (proximal much shorter) and apically with five strong elements (two geniculate). Exopod minute, cylindrical, about 2.4 times as long as wide, unornamented but armed with single unipinnate apical seta, about 2.4 times as long as segment.

Mandibula (Fig. 67E) with narrow cutting edge on elongated coxa, armed with at least one complex tooth ventrally, one unipinnate seta dorsally, and several smaller teeth and/or spinules between. Palp one-segmented, cylindrical, about 2.5 times as long as wide, unornamented, and armed apically with two smooth and subequal setae, each with pore on top.

Maxillula (Fig. 67F) with relatively small praecoxa, arthrite rectangular, about 1.4 times as long as wide in lateral view, unornamented but armed with lateral strong seta and four apical elements (probably three spines and one strong seta). Coxal endite armed with one smooth seta apically. Basis slightly longer than coxal endite, armed with two apical smooth setae. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 67G) unornamented, composed of syncoxa, basis, and one-segmented endopod. Syncoxa with two endites, each armed apically with two smooth setae, dorsal seta much longer. Basis drawn out into strong and smooth claw, without seta at base. Endopod represented by minute segment, basally fused to basis, armed with two smooth subequal apical setae.

Maxilliped (Fig. 67H) with very short syncoxa, unarmed and unornamented; basis slender, about 4.5 times as long as wide and almost nine times as long as syncoxa, unornamented and unarmed; endopod represented by short curved claw, swollen at base as indication of ancestral one-segmented endopod, unornamented, about 0.8 times as long as basis.

First swimming leg (Fig. 67I) with smooth praecoxa, coxa, and intercoxal sclerite. Basis somewhat shorter than coxa, pentagonal, unornamented, armed with single short seta on outer margin. Exopod three-segmented, armed with one outer spine on first segment and four elements on third segment (two outer spines and two apical geniculate setae); ornamented with few large spinules along outer margin on all segments and with frills on inner distal corners of first and second segments. Endopod two-segmented, about as long as exopod; first segment reaching slightly beyond distal margin of second exopodal segment, about four times as long as wide, unarmed, ornamented with two short rows of large spinules on outer margin and one long row on inner margin; second segment armed apically with long geniculate seta and much shorter spine; endopodal geniculate seta 1.5 times as long as entire endopod and 1.1 times as long as larger geniculate exopodal seta.

Second swimming leg (Fig. 67J) with smooth praecoxa, coxa, and intercoxal sclerite. Basis unarmed, ornamented with row of spinules on outer margin. Exopod three-segmented, ornamented with large spinules along outer margin, and with hyaline frills on each segment distally on inner side; first segment armed with one outer spine; second segment unarmed; third segment armed with three long elements (probably outer spine and two apical setae), innermost one about 1.7 times as



Fig. 67. *Parastenocaris savita*. Male: A. habitus, dorsal view; B. anal somite and left caudal ramus, lateral view; C. antennula; D. antenna; E. mandibula; F. maxillula; G. maxilla; H. maxilliped; I. first swimming leg; J. second swimming leg; K. third swimming leg; L. fourth swimming leg; M. fifth leg. Female: N. antennula; O. third swimming leg; P. fourth swimming leg; Q. fifth leg. Scales: 50 μ m (cited from Ranga Reddy, 2001, modified).

long as exopod; all exopodal armature bipinnate. Endopod one-segmented, cylindrical and short, about 3.7 times as long as wide, not reaching middle of first exopodal segment, ornamented with three large spinules along apical margin; armed apically with one smooth minute seta, about 0.5 times as long as segment and pointing inwards.

Third swimming leg (Fig. 67K) with smooth praecoxa, coxa, and intercoxal sclerite. Basis robust, armed with long outer seta and ornamented with diagonal row of large spinules close to outer margin. Endopod minute but distinct segment, about as long as largest spinules on outer margin but stronger, unornamented, and armed apically with smooth seta basally fused to segment. Exopod two-segmented; proximal segment about 2.9 times as long as wide, with small chitinous beak on distal part of inner margin, ornamented with single large spinule on outer margin distally, armed subapically with strong, smooth and complex spine, about as long as apophysis, lanceolate apically, with inner bulbous protrusion in distal part; distal segment (apophysis) only 0.4 times as long as proximal segment, bilobate apically, unarmed, and unornamented.

Fourth swimming leg (Fig. 67L) with smooth praecoxa, coxa, and intercoxal sclerite. Inner distal margin of basis produced into two processes; inner process narrower and less strongly sclerotised, smooth and parallel to endopod; outer process much broader and more strongly sclerotised, pointing outward, complex tridimensional structure, reaching beyond outer margin of endopod, and shielding proximal part of endopod. Exopod three-segmented, ornamented with few large spinules along outer margin on all segments, and with hyaline frills distally on inner side; first segment with concave inner margin, armed with single outer spine; second segment unarmed; third segment armed with outer spine and very long and strong apical seta; apical seta 1.2 times as long as entire exopod and 3.3 times as long as outer spine. Endopod one-segmented but constricted at middle, slightly shorter than first exopodal segment, with beak-like structure on top (probably formed by fused apical spine and spinule), curved inwards but distal beak pointing distally.

Fifth leg (Fig. 67M) simple rectangular cuticular plate, unornamented, armed with four smooth setae; outermost seta (ancestral basal one) longest, 3.8 times as long as entire leg; next seta (probably ancestral exopodal) about as long as leg; third seta from outer side (ancestral outer endopodal) 1.9 times as long as leg, and 1.4 times as long as innermost seta (inner endopodal). Fifth legs distinct at base, with very small space between them, and pointing caudally.

Sixth legs smooth, unarmed and unornamented, forming simple operculum covering gonopore.

Female: Body length, excluding caudal setae, from 440 to 470 μ m (460 μ m in allotype). Habitus, ornamentation of prosomites, colour, and nauplius eye similar to male, except genital and first abdominal somites fused into double somite and abdomen slightly less slender.

Genital double somite slightly longer than wide (ventral view), without trace of subdivision, with oval dorsal cuticular window in anterior half not larger than that in male. Genital complex occupying anterior ventral half of genital double somite; genital apertures closed off by vestigial sixth legs; median copulatory pores located between sixth legs; seminal receptacles small, difficult to distinguish from internal tissue and gut content; copulatory duct very short and weakly sclerotised. Third, fourth (preanal), and fifth (anal) urosomal somites similar to male.

Caudal rami similar to male but slightly shorter in proportion to anal somite and slightly wider at middle in lateral view; ornamentation and armature same as in male.

Antennula (Fig. 67N) also seven-segmented, unornamented, with slender aesthetasc on fourth segment, reaching beyond tip of appendage, and more slender apical aesthetasc on seventh segment, fused basally to two apical setae; both aesthetascs equally slender as in male; setal formula (possibly not complete): 0.4.4.2.1.0.9. All setae, except proximalmost one on second segment, smooth. Length ratio of antennular segments, from proximal end, 1:2.8:1.6:1:0.6:0.9:1.5.

Antenna, mandibula, maxillula, maxilla, maxilliped, first swimming leg, second swimming leg, and exopod of fourth swimming leg (Fig. 67P) similar to male.

Third swimming leg (Fig. 67O) with large praecoxa, smooth coxa and intercoxal sclerite. Basis ornamented with single large spinule on outer margin distally, armed with very long and smooth outer seta, longer than first exopodal segment. Exopod two-segmented, ornamented with large spinules along outer margin, both segments with hyaline frills distally on inner side; first segment armed with single outer spine; second segment with outer spine and apical strong seta; all elements bipinnate. Endopod one-segmented, small, curved outwards, unornamented, armed with apical strong spine, fused basally to segment, not reaching distal margin of first exopodal segment in length.

Fourth swimming leg (Fig. 67P) without spiniform processes on basis. Endopod one-segmented, ornamented with transverse apical row of five spinules at base of apical spine, distinct at base, bipinnate, and about as long as endopod; endopod reaching middle of second exopodal segment in length. Exopod similar to male.

Fifth leg (Fig. 67Q) also simple cuticular plate, but with inner distal corner produced into long and spiniform process, and ornamented with three spinules on inner margin. Armature same as in male.

Sixth legs vestigial, simple cuticular plates, covering gonopores, unornamented and unarmed.

TYPE: Type material in the Natural History Museum in London.

TYPE LOCALITY: India, Andhra Pradesh, River Krishna at Vijayawada, near bridge at Kanaka Durga Varadhi, interstitial 10 m from water edge and at a depth of 2.5 cm, fine sands.

DISTRIBUTION: This species is known only from the type locality, River Krishna at Vijayawada, India.

ECOLOGY: It was collected from fine sands on a river bank, about 10 m from the water's edge, at a depth of about 2.5 cm. It lives sympatrically with *P. sandhya* Ranga Reddy, 2001, not very closely related and lives in the deeper substrate, between 5 and 50 cm. This would imply that the two species occupy two different ecological niches. This sample was taken in August, while both species were displaced in February by another parastenocarid, *P. gayatri* (see above), closely related to *P. savita*.

REMARKS: The presence of dorsal cuticular windows on the anal somites and the shape of the fourth leg basis and endopod clearly place this species in the *brevipes* group of Lang (1948). In the original description, Ranga Reddy (2001) remarked that *P. savita* is probably most closely related to *P. gayatri*, but can be distinguished by the ornamentation of caudal rami and fifth leg in female, shape of the second leg endopod in female, and especially by the shape and ornamentation of the third and fourth legs in male. Dorsal cuticular windows are also more pronounced in *P. gayatri*, and there is an additional window on the genital somite in male and a larger one (derived from the fusion of two ancestral windows) in female.

43. Parastenocaris singhalensis Enckell, 1970 (Fig. 68)

Parastenocaris singhalensis Enckell, 1970, p. 551, figs. 31-34.

Male: Total body length of holotype specimen, measured from tip of rostrum to posterior margin

of caudal rami (excluding caudal setae), $340 \ \mu$ m. Information about specimen colour, nauplius eye, and habitus shape not available. Judging from drawings of anal somite and caudal rami (Fig. 68A), habitus probably cylindrical and very slender, without demarcation between prosome and urosome, and somites without expansions laterally or dorsally, all connected by well-developed arthrodial membranes. Hyaline fringes of somites smooth, very narrow and difficult to distinguish from arthrodial membranes. Integument weakly sclerotised, smooth, ornamented only with sensilla and pores (no cuticular pits or spinules). Presumably preanal somite and three anterior somites with large, oval dorsal cuticular windows, just as in *P. irenae* Enckell, 1970 (see above). Anal somite (Fig. 68A) ornamented only with pair of dorsal sensilla at base of anal operculum. Anal operculum (Fig. 68A) well developed, unornamented on outer surface, with straight caudal margin, reaching posterior end of anal somite. Anal sinus widely opened, without ornamentation.

Caudal rami (Fig. 68A) about 3.1 times as long as greatest width (lateral view) and about as long as anal somite, more or less cylindrical, but inflated in anterior third (from lateral view), armed with seven armature elements (three lateral, one dorsal, and three apical), without ornamentation. Dorsal seta slender and smooth, inserted at midlength and somewhat closer to inner margin, about 0.6 times as long as caudal ramus, probably triarticulate basally. Lateral setae thin and smooth, inserted relatively close to each other, approximately at 3/5 of ramus length. Proximal lateral seta inserted most dorsally, about three times as long as middle and distal setae (which are subequal), and about half as long as ramus. Inner apical seta very slender, smooth, inserted more ventrally, half as long as ramus. Middle apical seta strongest, without breaking plane, length unknown. Outer apical seta much smaller than middle apical seta, but also strong and without breaking plane, smooth, slightly longer than ramus.

Rostrum, antennula, antenna, labrum, paragnaths, mandibula, maxillula, maxilla, maxilliped, and first swimming leg unknown, but presumably similar to those in type species.

Second swimming leg composed of praecoxa, coxa, intercoxal sclerite, basis, three-segmented exopod, and one-segmented endopod; similar in shape, armature, and ornamentation to that of *P. irenae* and *P. noodti* Enckell, 1970 (see above). Endopod ornamented apically with three large spinules and armed with single smooth seta.

Third swimming leg (Fig. 68B, C) with robust basis, ornamented with row of eight long spinules along outer margin, and additional row of four smaller spinules on anterior surface. Endopod probably absent. Exopod with both segments fused; ancestral proximal segment about twice as long as wide, with large chitinous beak on inner margin and slightly convex outer margin, ornamented with row of cuticular pits or small spinules on inner beak, armed subapically with smooth and curved spine, twice as long as apophysis; ancestral distal segment (apophysis) small, oriented inward, complex trilobite structure.

Fourth swimming leg (Fig. 68D) composed of praecoxa, coxa, intercoxal sclerite, basis, threesegmented exopod, and one-segmented endopod. Inner distal margin of basis produced into two processes; inner process larger, smooth and curved outwards, simple spiniform structure, parallel to endopod and pointing distally; outer process somewhat smaller, but more strongly sclerotised, pointing outward, reaching outer margin of endopod, and shielding proximal part of endopod. No other ornamentation on basis. Exopodal armature and ornamentation presumably similar to that in type species, i.e., with one outer spine on first segment, no armature on second segment, and two elements on third segment; all exopodal segments probably with hyaline frills distally on inner side. First exopodal segment with concave inner margin, three times as long as greatest width, with stout outer distal spine, about 0.7 times as long as segment. Endopod one-segmented, very inflated basally from anterior view, slightly shorter than first exopodal segment, and almost parallel to it,



Fig. 68. *Parastenocaris singhalensis*, Male. A. anal somite and left caudal ramus, lateral view; B. third leg; C. distal part of third leg, different view; D. basis, endopod, and first exopodal segment of fourth leg; E. fifth leg. Scales: 50 μ m (cited from Enckell, 1970, modified).

armed with single smooth and curved seta apically (broadly fused basally to segment), ornamented with transverse row of four large spinules at 2/3 on anterior surface. Endopod and inner basal cuticular processes forming complex tridimensional structure.

Fifth leg (Fig. 68E) simple trapezoidal cuticular plate, inner distal margin not produced posteriorly into spiniform process, ornamented with single spinule next to basal seta, armed with three smooth setae; ancestral basal seta (outermost one) longest, about 1.4 times as long as two subequal endopodal setae, and 1.7 times as long as leg.

Sixth legs unknown, probably very similar to type species.

Female: unknown.

TYPE: Type material lost.

TYPE LOCALITY: Sri Lanka, Sabaragamuwa Province, Bopathella Falls, 14.5 km east of Ratnapura, interstitial in a sandy bank below the falls and surrounded by water.

DISTRIBUTION: Known only from the type locality, Bopathella Falls near Ratnapura, Sabaragamuwa

Province, Sri Lanka.

ECOLOGY: Only one male was collected at the type locality, and it is possible that the prime habitat of this species was not sampled. *Parastenocaris singhalensis* lives together with three other parasteno-caridids, all of which are relatively closely related.

REMARKS: The shape of the fourth leg basis and endopod would suggest that *P. singhalensis* belongs to the *brevipes* group of Lang (1948). Enckell (1970) recognised this, and also remarked on a certain resemblance of this species to *P. feuerborni* from Sumatra, especially in the shape of the male fourth leg endopod, ornamented with transverse row of large spinules that form a comb-like structure. The two species can be distinguished by the number of these spinules, but also by a very different shape of the male third leg, in addition to some differences in the ornamentation and armature of the caudal rami. *Parastenocaris singhalensis* differs additionally from all other Sri Lankan species by the presence of three lateral setae on the caudal rami. The shape of the male fifth leg is relatively similar to that of *P. lanceolata*, but the two species have a different endopod of the fourth leg, as well as the third leg. The latter is different from all Sri Lankan species of the *brevipes* group in that the apophysis is shorter than the first exopodal spine.

Key to species of the brevipes group

Currently 18 valid species could be recognized in the *brevipes* group, and a key to aid in their difficult determination is given below. It is adopted and augmented from Karanovic (2005a) and based solely on the morphology of males, since females of *P. brincki*, *P. lanceolata* and *P. singhalensis* are still unknown.

1.	Caudal ramus without unguiform process2
_	Caudal rami with unguiform process posteriorly P. muvattupuzha
2.	Third leg in adult male without endopod
_	Same appendage with endopod
3.	Endopod of third leg reduced to single seta
_	Endopod of third leg small but distinct segment
4.	Fourth leg endopod unarmed
—	Same segment with bipinnate apical spiniform element P. jane
5.	Endopod of fourth leg with transverse subapical row of 3 long spinules P. feuerborni
—	Same segment with longitudinal row of 5–6 long setules P. kimberleyensis
6.	Fifth leg with inner-distal corner protruding posteriorly as spiniform process7
_	Same appendage lacking spiniform process
7.	Fifth leg armed with only 2 setae ······ P. brincki
—	Same leg armed with 4 setae ······ P. palmerae
8.	Endopod of fourth leg 2-segmented, ending with 2 apical spinules
_	Same ramus 1-segmented, ornamented with more than 2 spinules 10
9.	First exopodal segment of third leg lacking subapical spine P. longipoda
_	Same segment with well developed spine apically on outer margin P. savita
10.	First exopodal segment of third leg armed with large dentate process on inner margin P. gayatri
—	Same segment with smooth inner margin 11
11.	Endopod of third leg minute spiniform element 12
_	Endopod of third leg slender seta P. brevipes
12.	Anal operculum convex; anal somite 1.6 times as long as caudal rami P. biwae

-	Anal operculum deeply concave; anal somite 1.9 times as long as caudal rami P. koreana
13.	Anal operculum smooth ······ 15
—	Anal operculum with row of spinules
14.	Endopod of fourth leg in male conical and smooth P. oshimaensis
_	Same ramus sickle-shaped, with 1 long spinule P. hinumaensis
15.	Fifth leg with inner-distal corner protruding posteriorly as spiniform process P. irenae
_	Same appendage lacking spiniform process
16.	Anal somite with 2 dorsal rows of spinules P. noodti
_	Anal somite lacking ornamentation
17.	Endopod of fourth leg with 4 long spinules P. singhalensis
_	Same ramus smooth, conical, sharply pointed P. lanceolata

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POSTSCRIPT

- After this manuscript was already completed Ranga Reddy (2011) described two new species from India that also belong to the brevipes group: *Parastenocaris sultej* Ranga Reddy, 2011 and *P. gundlakamma* Ranga Reddy, 2011.
- Ranga Reddy, Y., 2011. Two new hyporheic parastenocarididae from India *Parastenocaris sultej* n. sp. and *P. gundlakamma* n. sp. (Copepoda, Harpacticoida). Crustaceana Monographs, 16: 461–478.

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