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PHYLOGENETIC SYSTEMATIC OF *REMANEICARIS*

JAKOBI (COPEPODA, HARPACTICOIDA,

PARASTENOCARIDIDAE) FROM THE NEOTROPICAL

REGION.

PAULO HENRIQUE COSTA CORGOSINHO

MANAUS, AMAZONAS

APRIL, 2007

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**PHYLOGENETIC SYSTEMATIC OF *REMANEICARIS* JAKOBI
(COPEPODA, HARPACTICOIDA, PARASTENOCARIDIDAE)
FROM THE NEOTROPICAL REGION.**

SUPERVISOR: DR. EDINALDO NELSON DOS SANTOS SILVA

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Synopsis:

The Neotropical genus *Remaneicaris* was studied and almost all species previously described by Noodt (1962, 1963, 1965 e 1972), Kiefer (1936 e 1967) and Dussart (1983) were redescribed. Eight new species were described and added to this genus. The phylogenetic position of the genus *Remaneicaris* within the family, as well as the kinship between the species within this genus are for the first time discussed on the light of a Hennigian phylogenetic analysis.

Keywords: Phylogeny, redescription, Neotropis, Parastenocarididae, meiofauna.

This thesis is dedicated to my daughter Ana Luiza

César Corgosinho.

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Resumo

O gênero *Remaneicaris* é o grupo mais diverso de parastenocaridídeos da América do Sul, sendo composto por 28 espécies, mais oito novas espécies descritas neste trabalho. O grupo é monofilético e resultou ser basal dentro da família, sendo sua posição filogenética testada pelo método da sistemática filogenética de Hennig. Com isto, são feitas algumas considerações a respeito do “groundpattern” dos Parastenocarididae. Os *Remaneicaris* podem ser facilmente caracterizados pela posição subdistal do espinho externo do exopodito 3 da pata 4, bem como, devido a outros caracteres bem plesiomórficos, como a presença de duas cerdas no endito proximal da Mx2 e a presença de um endópodo unissegmentado na pata 3 dos machos. Uma nova subfamília é proposta aqui para acomodar o gênero *Remaneicaris*, compartilhando com este a mesma diagnose. Finalmente, é oferecida uma diagnose para cada um dos grupos monofiléticos dentro de *Remaneicaris*, sendo feita a redescrição de quase todas as espécies previamente descritas para o gênero. É fornecida também uma chave para a identificação das espécies.

Abstract

The genus *Remaneicaris* is the most speciose genus in South America, being composed by 28 species, plus six new species described here. It is monophyletic, and its position within the family Parastenocarididae is tested using the method of cladistic systematics. The genus turned out to be basal within the family and some remarks on the groundpattern of Parastenocarididae are given here. It can be easily characterized by the subdistal position of the outer spine of leg 4 exp 3 and other plesiomorphic characters, such as the presence of two setae on the first endite of Mx2 and a unisegmented endopod on the leg 3 of males. A new subfamily is proposed here to accommodate the genus *Remaneicaris*, sharing with it the same diagnosis. Finally, a diagnosis for each of the monophyletic groups within *Remaneicaris* and a redescription of most of the species previously described are here given. A key for the identification of the species is offered also.

Summary

This work is divided in a general introduction, six chapters formatted as scientific manuscripts and a general conclusion organized to give to the reader an idea of the species diversity and morphological diversity found within the genus *Remaneicaris*, about its phylogenetic relationships within the family Parastenocarididae, as well as about the kinship between the species that compose the mentioned genus.

Thus, in the general introduction (pages 1 to 12), the author intends to clarify the problem involved around the systematic of the parastenocaridids and, mainly, around the genus *Remaneicaris*.

The first chapter (pages 15-42) entitled “Two new interstitial species of *Remaneicaris* Jakobi 1972 (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro River, Minas Gerais, Brazil, with a redefinition of the genus.”, by Corgosinho and Martinez Arbizu (2005), deals with the “revalidation” of the genus, on the basis of a hypothesis of monophyetic supported by some characters not previously seen in any other member within the family. Some important characters such as the presence of lateral integumental windows on some urosomites, the absence of intercoxal sclerite on leg 5 and the structure of leg 4 are discussed here. A new diagnosis based also on synapomorphies and an updated list of species within the genus (until the date of publication) is also provided here.

The second chapter (pages 44-84) entitled “Three new species of *Remaneicaris* Jakobi 1972 (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro River, Minas Gerais, Brazil, with some remarks on the groundpattern of Parastenocarididae”, by Corgosinho, Martinez Arbizu and Santos Silva (2007), suggests how the groundpattern of Parastenocarididae should be, based on the observation of some plesiomorphic structures that can be found in the species that compose this genus.

On the third chapter (pages 86-106), entitled “Redescription of *Remaneicaris ignotus* (Dussart, 1983). A Parastenocarididae (Copepoda, Harpacticoida) with an unusual set of plesiomorphic characters.”, by Corgosinho, Martínez Arbizu and Santos Silva (in press), both sexes of *R. ignotus* (Dussart 1983) are redescribed and, due the presence of some plesiomorphic structures for the family, even considering the remaining species of the genus *Remaneicaris*, the possibility that this species should be considered the most basal taxon within *Remaneicaris* is discussed. The importance of some characters, such as the presence of dorsal integumental windows from the 2nd to the 5th urosomite and the presence of an inner seta on the basis of leg 1 are exhaustively discussed here.

The fourth chapter (pages 108-130) entitled “Three new interstitial species of *Remaneicaris* Jakobi 1972 (Copepoda, Harpacticoida, Parastenocarididae) closely related to the species around *R. analuizae*” by Corgosinho, Martínez Arbizu, Calixto and Santos-Silva, deals with the description of three new species of *Remaneicaris* of the *analuizae*-group, and their characters are discussed within a phylogenetic context. All the references to the monophyletic groups within *Remaneicaris* are put within quotation marks, since the formal proposition of each group is only performed on the next chapter.

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Introduction

Harpacticoid copepods are small benthic Crustacea, usually smaller than 1.0 mm, thus being classified as meiofauna. Almost all families of Harpacticoida occur in marine environments, from tidal zones to abyssal deeps (Lang 1948). On sandy beaches, some families have invaded marine mesopsammic habitats (Higgins and Thiel 1988; Martínez Arbizu and Moura 1994).

Only a few families (Phyllognathopodidae Gurney, 1932, Chappuisiidae Chappuis, 1949, Ameiridae Monard, 1927, Canthocamptidae Sars, 1906 and Parastenocarididae Chappuis, 1933) have succeeded in colonising freshwater environments (Dussart and Defaye 1990; Rouch 1986).

Contrasting with the Canthocamptidae that are mainly epibenthic organisms, the Parastenocarididae are especially well adapted to interstitial life in the hyporheic zones of rivers as well as to life in continental aquifers. Their bodies are vermiform, and their lengths vary between 250 μm and 500 μm . They are completely transparent and have no eyes. In accordance with Hosfeld and Schminke (1997), they present osmoregulatory organs called integumental windows on cephalotoraxic and urosomal segments.

The sister group of Parastenocarididae, the genus *Psammonitocrella* Rouch, 1992, also occurs in hyporheic habitats. Because of this, Martínez Arbizu and Moura (1994) postulated the origin and diversification of parastenocaridids within continental groundwaters. As proof of Parastenocarididae in phreatic waters, Martínez Arbizu (pers. com.) collected these organisms from groundwater (at about 100 m) in Spain, and Bozic (1978) found Parastenocarididae in samples taken from subterranean waters in the Sahara desert.

Approximately 97% of the continental freshwaters are subterranean (Marmonier *et al.* 1993). The colonisation of interstitial environments and of groundwaters probably allowed parastenocaridids to remain relatively protected from earth climatic changes that occurred at a geological scale. So, despite of the possible effect of rainfall variation on river hydrological regime,

resulting in the union or the separation of some water bodies and even the drying up of some of them, the aquifers remain practically unaltered. In Brazil aquifers as refuge areas probably were more important in the regions of the Central Brazilian and Guyana shields, since these areas were not covered by marine incursions that occurred during the orogenesis of South America prior to its separation from Africa about 100 million years ago (Lundberg *et al.* 1998). From another point of view, the isolation of hydrographic basins due to geomorphological changes could act as an important vicariant process that influenced the diversification of this family. For South America we can mention the uplift of the Andes that promoted great changes in the drainage patterns of almost all South American rivers.

Parastenocarididae are typical freshwater organisms. There are only a few derived species that exhibit a secondary resistance to euryhaline conditions (Noodt 1962; Enckell 1969). Thus, the formation of epicontinental seas in South America (revised in Lundberg *et al.* 1998) may have promoted the extinction of an expressive number of Parastenocarididae species in the flooded areas, allowing the dispersion of a few more tolerant species along their coast.

The family Parastenocarididae is, without doubt, monophyletic, being characterised and easily distinguished by the sexual dimorphism present on the third pair of pereopods. As an apomorphy, the males have these appendices modified in a grasping organ, which allow the capture of the female during copulation (Glatzel 1990). Beyond the dimorphism of the third pereopod, the males present other modifications, mainly on the endopod of the fourth leg and, sometimes on the first, second, fifth pereopod and furca (Schminke 1991). All of these modifications constitute important characters used to distinguish species and genera.

Despite its monophyletic condition, the phylogenetic position of parastenocaridids arose some controversy in the past (*viz.* Kessler 1913; Schnitter and Chappuis 1914; Monard 1927; Pesta 1932; Chappuis 1933; Kunz 1938; Lang 1948; Martínez Arbizu and Moura 1994 and Bruno *et al.*

1998) and within the family, different supraspecific groups (viz. Chappuis 1937; Kunz 1938; Lang 1948; Noodt 1962; Noodt 1963 and Noodt 1972), or genera (Jakobi 1969, 1972a and 1972b) have been created. Thus, following the Germanic tradition, Chappuis (1937) tried to separate different species of *Parastenocaris* Kessler, 1913 in four distinct groups on the basis of the morphology of the basis and endopod of male leg 4. Later, Lang (1948) revised Chappuis' system and proposed the groups *brevipes*, *minuta*, *nana*, *cujensis*, *musciicola*, *fontinalis* and *staheli*, adopting also the group *proserpina* of Kunz (1938). Noodt (1962, 1963 and 1972b) added five more groups to the system of Lang (1948), being them the groups *panamericana* (Noodt 1962), *forficata* (Noodt 1963), *sioli* (Noodt 1963), *remanei* (Noodt 1963) and *columbiensis* (Noodt 1972b). Although weakly based on synapomorphies, the system of Lang (1948)-Noodt (1962, 1963 and 1972b) still is the best of what we have and most of the groups can be easily recognised and reworked toward monophyletic unities.

Of particular interest, we can mention the work of Jakobi (1972a). In this paper, the author proposes the creation of 26 new genera based on the morphology of the endopod of male leg 4. Some of these new genera were based on the groups of species previously proposed by Lang (1948) and Noodt (1962, 1963 and 1972b). However, most of them were not accepted by subsequent authors (i.e. Rouch 1986; Dussart and Defaye 1990; Ahnert 1994; Reid 1994; Reid 1998 and Galassi and De Laurentiis 2004), mainly due to the heterodox system adopted by Jakobi (1972a). His classification was severely criticized by Schminke (1976), since it is based in an orbital system (analogous to the orbital scheme of the chemical elements) and not in a phylogenetic argumentation. The most problematic result of Jakobi's "Schalenmodell" system was the creation of paraphyletic and polyphyletic groups (based on plesiomorphies or homoplasies), since similar complex structures were not considered homologous *a priori*, but as being result of independent processes (parallelisms and convergences).

Notwithstanding of their creation based on a system considered as invalid on the phylogenetic point of view, Jakobi (1972a), on the act of creation of these new genera, offered a diagnosis and designated a valid type species for each one of the 26 genera, thus, the ICZN rules applies (article 13 from ICZN 2000). Consequently, all the genera created by Jakobi (1972a) are valid and should be used, demanding, however, a future revision based in a robust phylogenetic argumentation.

Albeit of the unacceptance of most of Jakobi's genera, *Forficatocaris* Jakobi, 1969 and *Paraforficatocaris* Jakobi 1972 (junior synonym of *Brasilibathynellocaris* Jakobi, 1972 (Corgosinho and Martínez Arbizu in prep.)) were fully adopted and, paradoxically, remained almost as a consensus the use of Lang (1948) and Noodt (1962, 1963, 1972b) "systems" in posterior works. Later Schminke (1993; pers. comm.) correctly accepted the genus *Cafferocaris* Jakobi, 1972 as being monophyletic after short amendment. Other genera (viz. *Potamocaris* Dussart, 1979; *Murunducaris* Reid, 1994 and *Simplicaris* Galassi and De Laurentiis, 2004), however, were created and accepted without, or with a superficial phylogenetical reasoning, basing their creation only on the observation of synapomorphies. Thus, despite of the validity of this practice, we should be aware that, albeit of the quality of synapomorphies for the definition of monophyletic unities, they do not exclude the possibility that a given monophylum belongs to a bigger monophyletic group that, hence, can be managed toward a paraphyletic status when we force the creation of a new genus without the knowledge of the whole scenario around it.

At about 241 species of Parastenocarididae were already described. Circa of 69 occur on the Neotropical region, as representatives of the genera *Parastenocaris*, *Remaneicaris* Jakobi, 1972, *Brasilibathynellocaris*, *Forficatocaris*, *Pararemaneicaris* Jakobi, 1972, *Siolicaris* Jakobi, 1972, *Paraforficatocaris*, *Potamocaris* and *Murunducaris*. Despite the relatively great number of species described, there are only few works dealing with the phylogenetic relationships of species within

monophyletic groups or between the monophyletic groups inside the family Parastenocarididae. Only one monograph can be cited for the Neotropical region. In this work Ahnert (1994) studied the phylogenetic relationships between species of *Forficatocaris*, redescribing all species previously described by Noodt (1962, 1963) and describing two new species (unfortunately not published until now).

The first studies about South American parastenocaridids started with Menzel (1916), with the description of *Parastenocaris staheli* Menzel, 1916 from Surinam and Delachaux (1924), who described *P. chelifera* Delachaux, 1924 also from Surinam. For *Remaneicaris*, the first described species was *R. hexacantha* (Kiefer, 1936), from northeastern of Brazil. Later Jakobi and Silva (1962) described *R. hurdi* (Jakobi and Silva, 1962) from the southern of Brazil, while Noodt (1962) described *R. palaciosi* (Noodt, 1962) and *R. meyerabichi* (Noodt, 1962) from samples taken in El Salvador (Central America).

In South America, the most diverse genera are *Remaneicaris* (50% of the species), *Forficatocaris* (20%) and *Potamocaris* (10%). With 34 species, *Remaneicaris* is the most diverse genus, being widely distributed, with members on Central America and southern of South America. This genus was proposed by Jakobi (1972a) to accommodate the species included by Noodt (1963 and 1965) in the *remanei*-group, together with some other few Neotropical species from different evolutionary lineages.

When we exclude some few unrelated species, previously included by Jakobi (1972) within *Remaneicaris*, the genus in the concept of Noodt's *remanei*-group is monophyletic and can be well characterized by the presence of a subdistal spine on the outer margin of the third exopodite of the leg 4, as well as by the presence of a long outer spinule on the medial portion of exopodites 2 and 3 of legs 2 and 4 and the absence of intercoxal sclerite on the leg 5 (Corgosinho and Martínez Arbizu

2005). However, even Noodt (1969) and later Jakobi (1972a) distrusted its natural condition. For example, in his work entitled “Die Grundwasserfauna Südamerikas”, Noodt (1969) wrote:

“Especially widely distributed (from Patagonia to Central America) we find the remaneicaris-group Noodt, with numerous species that, however, are obviously not homogeneous and need to be splitted in the future.”
(“Besonderers weit verbreitet (Patagonien bis Zentral-Amerika) ist die remanei-gruppe Noodt mit bereits zahlreichen Arten, die jedoch offenbar noch inhomogen ist und weiterer Unterteilung bedarf”).

Probably the belief about the non monophyly of *Remaneicaris* arose due to the high morphological diversity that can be seen in this genus, being composed by different monophyletic unities with distinct evolutionary tendencies (ex: shape of the leg 3 and endopod of males' leg 4). This probably conditioned Jakobi (1972a) to include in *Remaneicaris* the species *P. staheli* Menzel, 1916, *P. itica* Noodt, 1962 and *P. dactyloides* Kiefer, 1967, while *R. membranacea* (Noodt, 1965) was relocated to the genus *Pararemaneicaris* Jakobi, 1972, together with other non *Remaneicaris* species such as *Brasilibathynellocaris cuscatensis* (Noodt, 1962) and *P. santaremensis* Noodt, 1963.

Apart from some synapomorphies in different levels of generality, the genus *Remaneicaris* can be also easily differentiated from other genera due to the presence of some plesiomorphic characters that have never been observed in other parastenocaridids. In this context we can mention the presence of a unisegmented male endopod in leg 3 of almost all species, the presence of two setae on the first endite of the Mx2 and three slender setae on the second endite of the Mx2. Following this, in chapter 5 it is suggested that *Remaneicaris* is the most basal group within the family and that should compose a subfamily independent from those proposed by Schminke (1993).

Despite of the presence of some easily identifiable characters, such as the plesiomorphies and apomorphies mentioned above, the study of this genus raises some problems regarding the phylogenetic relationships between the monophyletic groups within this genus and between the species that compose it. Therefore, some times the decisions could only be taken based on the fine ornamentation of the appendices or of other characters previously not figured on the original descriptions.

The family Parastenocarididae is widespread over all continents, with the exception of Antartida and Tasmania Islands (Schminke, 1981). Because of this, it is reasonable to believe that this small group of crustaceans was widely distributed along the whole Pangea prior to the drift of its tectonic plates. On the northern hemisphere some groups show a Holarctic distribution (Reid, 1995), while on the south, some monophyletic groups are distributed over wide portions of Gondwana (Schminke, 1981). Thus, the sister groups of endemic Neotropical genera should be searched in Africa or even in the neotropis. In this sense, it is very interesting the presence of *P. ahaggarica* Bozic, 1978 Africa. This parastenocaridid shows several characters in common with *Remaneicaris* and could be easily allocated to it, except for the presence of a much-modified Mx1, never observed before in any species of the family Parastenocarididae. Hence, until the redescription of this species, the wisest assumption is to consider it as *incerta sedis* within *Remaneicaris*.

Only monophyletic groups have a common ancestrality and a single evolutionary history. Since the history of diversification of a monophyletic group is correlated with geological events, first it is necessary to develop a robust hypothesis about the possible monophyletic groups within Parastenocarididae that, together with a knowledge of the distribution of these groups can be the base for a posterior biogeographical analysis of this family in the neotropical region.

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Objectives

The knowledge of the real diversity of parastenocaridids in the Neotropical region, as well as its biogeography and kinship relations between monophyletic groups is very scarce. Wide areas of South America remain unexplored, mainly the Amazonic basin, northeast region of Brazil, Colombia, Venezuela and Guyana, west of Andes (Equator, Peru and Chile) and the Austral subregion.

The main objective of this work is to increase the knowledge about the diversity, distribution and phylogenetic relationships between the species of *Remaneicaris* and between this genus with the remaining parastenocaridids.

Specific objectives

- Description of the new species of *Remaneicaris*.
- Study and redescription of the type species already described.
- Propose a diagnosis for the genus, based also on autoapomorphies.
- Definition of the systematic position of the genus *Remaneicaris* within the Parastenocarididae.
- Definition of the monophyletic groups inside *Remaneicaris* and the establishment of a hypothesis of phylogenetic relationship between these groups.

Chapter I

Two new interstitial species of *Remaneicaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro River, Minas Gerais, Brazil, with a redefinition of the genus.

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Abstract

Members of the copepod genus *Remaneicaris* Jakobi, 1972 are reported for the first time from the state of Minas Gerais, southeastern Brazil. Two new species were discovered in interstitial near-shore waters of the small river Ribeirão do Ouro (tributary of the Paraopeba River of the São Francisco hydrographic basin). *Remaneicaris analuizae* n. sp. and *R. euniceae* n. sp. are described in detail, and their phylogenetic relationships within the genus discussed. The species differ from each other by the shape of endopod of leg 2, shape of leg 3 exopod, armature of leg 5, ornamentation of the telson, and by the number of integumental windows and sensilla. The monophyletic status of the genus is discussed and an updated list of species provided. The geographical occurrence of the genus in South America is briefly reviewed.

Keywords: Copepoda, Parastenocarididae, *Remaneicaris*, hyporheos, Neotropis, phylogeny.

Introduction

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Harpacticoid copepods belonging to the family Parastenocarididae Chappuis, 1933 are typical meiofaunal components of freshwater subterranean waters. They represent, together with members of the Canthocamptidae Brady 1880, the most successful group of benthic fresh-water harpacticoids in terms of both diversity and abundance. For example Reid (1993) recorded 43 species of Harpacticoida from a “campo úmido” (hillside flush marsh) in Brasília, Brazil, 18 of them Parastenocarididae (16 new to science). Further, Noodt (1963, 1965, 1972) found as many as 16 new species of Harpacticoida in South and Central American interstitial habitats.

Despite their presumable importance, very little is known about the actual diversity of Parastenocarididae in Neotropical countries, nor about their role in freshwater ecosystems. This may be the consequence of the traditional devotion of most South American limnologists to the study of lakes and reservoirs, neglecting non-planktonic habitats.

Currently, the Brazilian parastenocaridid fauna encompasses 31 known species (Reid 1998). In this study we describe two new species of the genus *Remaneicaris* collected from the hyporheic zone of one stream, Ribeirão do Ouro, belonging to the São Francisco River basin, in Florestal, Minas Gerais, Brazil. This represents the first record of *Remaneicaris* for the state of Minas Gerais. We favour the revalidation of the genus *Remaneicaris*, arguing for its monophyly. A list of current valid species of the genus is provided, based on literature descriptions.

Material and Methods

The samples were taken next to the river bank using the Karaman-Chappuis method (Chappuis 1942) using a 100 µm mesh, stained with rose bengal, and fixed with formalin at a final concentration of about 4%.

Animals were dissected in lactic acid and mounted on slides in glycerine. Drawings were made with an Olympus microscope, using a drawing tube, at 400x and 1000x magnification.

Abbreviations used are: ap= apomorphy, A1 = antennule, A2 = antenna, Ae = aesthetasc, Md= mandible, Mx1= Maxillulae, Mx2= Maxillae, Mxp= maxilliped, enp= endopod, exp= exopod, pl= plesiomorphy, P1-P5 = legs 1 to 5.

The type material is deposited in the invertebrate collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Descriptive part

Family Parastenocarididae

Genus *Remaneicaris*

Differential diagnosis: Parastenocarididae with 9-segmented antennule in male (pl) and 7-segmented antennule in female (pl). Male antennule haplocer (pl). Maxilla with 2 endites, proximal endite with 2 seta (pl). P1 endopod not sexually dimorphic (pl). P2 and P4 middle and distal exopodal segments with long spinule located mesially on outer margin (ap). P4 distal exopodal segment with distal outer seta shifted to subdistal position (ap). P3 male with endopodal segment bearing one seta (pl), apophysis rounded without setae (ap?). P4 male enp leaf-shaped and hirsute (ap?). P5 without sexual dimorphism (pl), displaced to ventro-lateral position (ap?) and lacking intercoxal sclerite (ap?). Furca with all three anterolateral setae located on distal third.

***Remaneicaris analuizae* n. sp.**

Type material: Holotype, one dissected male on 5 slides (INPA 1384).

Allotype, one dissected female on 7 slides (INPA 1385); paratypes, one male (INPA 1388) and two females (INPA 1386, 1387) mounted on 1 separated slide each.

Derivatio nominis: The species is named after the senior author's daughter, Ana Luiza Cesar Corgosinho.

Locus typicus: Ribeirão do Ouro, Sítio do Corgosinho, Florestal, state of Minas Gerais, Brazil.

Coordinates: 19°48'19S, 44°27'45W.

Male. Habitus (Fig. 1 A-B). Length 375 μm (measured from tip of rostrum to distal rim of anal operculum). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Presence of 1 dorsal integumental window on cephalothorax and second urosomite. Urosomites 4-5 with pair of lateral integumental windows. For sensilla on tergites see Fig. 1 A-B. Dorsal side of telson with 1 row of 10 spinules on proximal third; on the ventral side, with 2 pairs of spinules on proximal half, and 2 rows of 5 spinules near the insertion of the furca. Anal operculum ornamented with transverse row of 8 spinules. Anal field flanked by row of 3 spinules on right side and 5 spinules on left side. Furca (Fig. 2 A-C) about 4 times as long as wide, with 7 setae. All setae located on distal third. Ornamentation being composed by 3 dorsal spinules located on the proximal region of distal half of furca and 2 spinules on the distoventral margin. A1 (Fig. 3A) 9-segmented, haplocer and with a peculiar hyaline tip on distal segment; armature beginning with proximal segment: 0/5/4/1/5+Ae/1/3/1/9+Ae. A2 (Fig. 3 D) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing a ventral hyaline frill and 7 setae; the innermost setae lost on holotype but present on paratype (represented by a dotted line). Md, Mx1, and Mxp armature as *Parastenocaris hispanica* Martínez Arbizu 1997; proximal endite of Mx2 with 2 setae on the new species (Fig. 3 F). P1 (Fig. 4 A) coxa unarmed, with two rows of spinules on posterior side; basis with outer seta and 1 pore on anterior outer margin, 2 spinules on outer margin, and 3 spinules distally arranged; exp 3-segmented, segment 1 with one outer spine, segment 2 unarmed, segment 3 with 2 outer spines, 2 geniculated setae and a posterior pore; enp 2-segmented, segment 1 with 1 row of 6 long spinules along the inner margin and 2 rows of 3 shorter spinules on the outer margin, segment 2 with a hyaline frill and 2 setae distally arranged, 1 of them geniculated. P2 (Fig. 4 B) coxa unarmed, with 1

row of small spinules on the posterior side; basis without outer seta and ornamented with 1 row of spinules on the outer margin, 3 spinules distally placed and 1 pore on anterior outer margin; exp 3-segmented, segment 1 with an outer spine, segment 2 without setae, but with a row of spinules on the distal portion and one long spinule located mesially on the outer margin; segment 3 with 3 setae, a distal hyaline frill on the inner corner, one spinule located mesially on the outer side and one spinule in a subdistal position; enp 1-segmented and with 1 seta, enp ornamented with 2 distal spinules, and 3 spinules along the outer margin. P3 (Fig. 4 C) coxa unarmed; basis with an outer seta and a foliaceous hyaline structure proximal to the enp, on the inner margin; enp represented by 1 short spine; exp 1-segmented, elongated, bearing 2 minute spinules on the proximal inner margin and 2 rows of spinules along the outer margin; subterminally with 1 short curved seta (“thumb”) which is bifid at tip; apophysis short and rounded, softly trilobed. P4 (Fig. 4 D) coxa unarmed, with two small spinules on the posterior side; basis with outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 with an outer spine, segment 2 without setae, with a row of small spinules along the inner margin, a distal row and a long spinule located mesially on the outer margin, segment 3 armed with 1 apical seta and 1 subdistal seta, ornamentation being composed by a distal hyaline frill on the inner margin, one spinule located mesially on the outer margin and one subdistally arranged; enp 1-segmented, leaf-shaped, covered with numerous long spinules. P5 (Fig. 4 E) formed by a small, bilobed plate with 3 setae on the inner lobe and 1 seta on the outer lobe; intercoxal sclerite absent. P6 not discernible.

Female: Sexually dimorphic in A1, P1, P2, P3, P4, genital field and telson.

Female. Habitus (Fig. 1 C). Length 380 μm (from the tip of rostrum to the distal rim of operculum).

Anal operculum (Fig. 2 B) convex, ornamented with 13 spinules and flanked with 4 spinules on the right side and 5 on the left side. Telson with 1 row of 14 spinules on the proximal third of the dorsal

side, 2 rows of 2 spinules ventrally, on the proximal region and 2 rows of 4 spinules near the insertion of the furca. Furca (Fig. 2 B), ventrodiscal margin with 3 spinules, and with 2 additional rows of 4 short and 4 long spinules on the inner margin. A1 (Fig. 3 C) 7-segmented; armature beginning with the proximal segment: 0/4/5/2+Ae/1/1/9+Ae. A2 (Fig. 3 E) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae and a hyaline frill. P1 basis with two rows of three spinules near the insertion of the enp, enp 1 (Fig. 5 A) as in males, spinules along inner margin of first enp segment somewhat closer to each other. P2 (Fig. 5 B) as in males, with one pore on the basis and on the second exopodite; spinules on the outer margin of enp are somewhat longer. P3 (Fig. 5 D) coxa unarmed and with 1 row of spinules on the posterior side; basis with 1 outer seta and ornamented with 1 row of spinules near the insertion of the enp; exp 2-segmented, segment 1 with one outer spine, segment 2 with 1 spine, 1 seta and a proximal pore; enp 1-segmented and spiniform, with 2 spinules on the outer margin. P4 (Fig. 5 C) as in males, enp spiniform with 1 row of 3 spinules on the outer margin. P5 (Fig. 5 E) as in males. Genital field as illustrated in Fig. 5 E. Copulatory pores not discernible, but according to spermatophore position, a single mesially located copulatory pore is probably present. Gonopore is a transverse slit.

Variability

Male. Paratype 1: Telson with one dorsal row of 12 spinules on the proximal region; anal operculum ornamented with only 6 spinules and flanked with 4 spinules on each side.

Female. Paratype 2: Telson with one dorsal row of 12 spinules on the proximal region; furca with 5 distal spinules.

***Remaneicaris euniceae* n. sp.**

Type material. Holotype: 1 male, dissected and mounted on 5 slides (INPA 1389). Paratype: 1 male mounted on 1 slide (INPA 1390).

Derivatio nominis

The species is named after the senior author's mother, Eunice Helena Costa Corgosinho.

Locus typicus: Ribeirão do Ouro, Sítio do Corgosinho; Florestal, state of Minas Gerais, Brazil.

Coordinates: 19°48'19S, 44°27'45W.

Male (Fig 6 A-B). Length 315 μm (from rostrum to operculum). Rostrum with a large base and 2 sensilla on tip. Cephalothorax and second urosomite with 1 dorsal integumental window. Urosomite 5 with a lateral integumental window. Urosomite 4 without windows. Arrangement of sensilla on tergites illustrated in Figs. 6 A-B. Telson with one dorsal row of 9 spinules on the proximal region, 2 rows of 3 spinules on the ventral side, and 2 rows of 3 spinules distally arranged, near the insertion of the furca. Operculum convex without spinules, but flanked with 2 spinules on each side. Furca with 7 setae, all of them located on the distal third, 2 distal spinules, and 2 spinules dorsally arranged on the distal third. A1 (Figs. 7 A-D) 9-segmented, haplocer and with a peculiar hyaline tip; armature beginning with proximal segment: 0/5/4/1/5+Ae/1/3/1/9+Ae. A2 (Fig. 7 E) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing two hyaline frills and 7 setae; Mouthparts armature as in *Remaneicaris analuizae* n. sp.; P1 (Fig. 8 A) with fewer spinules (3 spinules) along inner margin of first enp segment, coxa with a posterior row of spinules, basis with three distal spinules on the anterior side and an outer pore. P2 (Fig. 8 B) enp bilobed with 1 seta and 2 terminal spinules on the outer lobe. P3 (Fig. 8 C), basis with an inner protuberance and 1 long curved seta representing the enp; exp with one row of 2 minute spinules proximally on the inner margin and a protuberance, thumb sigmoid, tapering distally, bifid at tip; apophysis with 2 small pointed protuberances on the outer margin. P4 (Fig. 8 D) similar to *R. analuizae* n. sp.; first exp

segment with a row of 5 spinules on the inner margin; enp leaf-shaped, covered with numerous long spinules on the proximal region and with a strong tip ornamented with a row of small spinules along the inner margin. P5 (Fig. 8 E) bilobed, inner lobe ending in a small spiniform process and bearing 3 setae, outer lobe with 1 seta.

Discussion

The genus *Remaneicaris* was proposed by Jakobi (1972) to accommodate the species included in Noodt's (1963) *remanei*-group, together with some other neotropical species described subsequently. *Remaneicaris* was based on a valid type species, viz. *Parastenocaris remanei* Noodt, 1963, and therefore it has to be considered a valid genus according to ICZN. But this and other of Jakobi's genera have not been accepted by subsequent workers. This is probably because of Jakobi's heterodoxic systematic method, the "Schalenmodell", in which similar complex structures were not considered a priori homologous to each other, but rather the results of convergence or parallelism within evolutionary trends. This methodology has been strongly criticized by Schminke (1976). We do not share most of Jakobi's ideas concerning the phylogeny and biogeography of Parastenocarididae. However, *Remaneicaris* represents a valid genus, and therefore must be used to group the species that constitute a monophyletic group around *R. remanei*. It would be a great mistake to describe the present species as "Parastenocaris", while other neotropical species are assigned to genera like *Forficatocaris* Jakobi, 1972, *Potamocaris* Dussart, 1970 and *Murunducaris* Reid, 1994. The type genus of the family Parastenocarididae has to be used exclusively for the monophyletic group around *Parastenocaris brevipes* Kessler, 1913. Recently Galassi and de Laurentiis (2004), while proposing the new genus *Simplicaris* Galassi and de Laurentiis, 2004, to accommodate two parastenocaridids from Italy, redefined the genus *Parastenocaris* sensu stricto. These authors proposed to retain within *Parastenocaris* Kessler, 1913 only those species belonging

to the *brevipes*-group as revised by Reid (1995). We agree with this argumentation and redefine the genus *Remaneicaris* (see above) to include only species phylogenetically related to *R. remanei*.

Unfortunately a robust hypothesis of the phylogenetic relationships within Parastenocarididae is far from completion. Therefore parastenocaridid species are sometimes assigned in genera using the exclusion principle, rather than synapomorphic characters. In our case, we propose to assign the new species to *Remaneicaris*, using three characters that we believe to be apomorphic at different evolutionary levels.

The first concerns the position of the outer spine on the third exopodal segment of leg 4. This spine is located terminally on the outer margin in almost all members of Parastenocarididae, while it is located subterminally on the outer margin in all the species that we presently assign to *Remaneicaris* (arrowed in Fig. 4 D). We consider the displacement of this spine a major apomorphy of this genus. The homologous seta is displaced also in the species *Parastenocaris spinosa* Wells, 1964, *P. spinipes* Wells, 1964 from Africa and *P. pusillus* Chappuis, 1954 and *P. trisaetosa* Chappuis, 1954 from Madagascar. We conclude that this displacement is the result of convergent evolution rather than a synapomorphy linking these species with the Neotropical *Remaneicaris*. The clue for this assumption is given by the type of modification and grasping of the male antennule. In *Remaneicaris* the male antennule is haplocer representing the symplesiomorphic condition of the family. The same type of antennule is present in the members of the so called “Fontinalicarididae” (Schminke 1993). While grasping the male moves the 8th against the 7th segment. The 9th (distal) segment is bent dorsally over the 5th segment. The geniculation mode of male antennule in *P. spinosa*, *P. spinipes*, *P. pusillus* and *P. trisaetosa* belong to special type where the 8th (penultimate) segment is transformed, displaying a strong process on inner distal margin. While grasping, the 8th segment is moved against the 7th and the 9th segment is moved outwardly and has no function in grasping. According to Schminke (1993, and pers. comm.) this type of antennule is a autapomorphy

of the “Parastenocaridinae”. *Remaneicaris* do not belong to the crown-group “Parastenocaridinae”, and therefore cannot be related to the species from Africa and Madagascar.

The second character involves the presence of a long cuticular spinule located mesially on outer margin of middle and distal exopodal segment on legs 2 and 4. This peculiar spinule (arrowed on Fig. 4 B) is present on all species assigned here to *Remaneicaris*, but is not present in other Parastenocarididae. We speculate that this spinule is shifted from the outer distal spinule row present in those segments in other Parastenocarididae.

The third character concerns the position of the integumental windows of the fourth and fifth urosomites. These thin cuticular areas are present in various freshwater and brackish-water crustaceans, and have an osmoregulatory function (Hosfeld and Schminke 1997). Reid (1994) reviewed the presence of these organs in Parastenocarididae. The presence of integumental windows seems to be a character present in the ground-pattern of Parastenocarididae according to the following pattern: 1 dorsal window on the cephalothorax and 1 dorsal window on urosomites 2-5 in the male and 2-4 in the female (due to the genital double-somite in the female). Variations in this pattern occur and have to be considered derived situations. Male *Murunducaris juneae* Reid, 1994, for instance, have lost the windows while these organs are still present in females of this genus (Reid 1994). Some African parastenocaridids, viz. *P. caffer* Chappuis, 1936, *P. madagascarensis* Chappuis, 1952, *P. forficulata* Chappuis, 1952 and *P. arenosus* Fryer, 1956, *P. aethiopica* Cottarelli and Bruno, 1995 (Chappuis 1936, 1952, Fryer 1956, Cottarelli and Bruno 1995) display lateral or ventro-lateral windows on the fourth and fifth urosomites. Besides these African species, the only parastenocaridids known to display lateral windows belong to the genus *Remaneicaris*. The shifting of these windows to the lateral position is not a character present in the ground-pattern of the genus, but it evolved within *Remaneicaris*. For example, *Remaneicaris ignotus* (Dussart, 1983) displays 1 dorsal window each on urosomites 2-5, while in *R. palaciosi* (Noodt, 1962) and *R. meyerabichi*

(Noodt, 1962) these urosomal windows extend from the dorsal to the lateral margins (Dussart 1983, Noodt 1962). All other *Remaneicaris* species, as far as described in detail, seem to have 1 dorsal window on the cephalothorax and second urosomite, and 1 lateral window on the fifth urosomite, as is the case in *R. euniceae* n. sp. (Figs. 6 A-B). The condition present in *R. analuizae* n. sp. is remarkable, because of the presence of a lateral window on the fourth urosomite (Fig. 1 A-C). It seems that there are several apomorphic characters involved in these transformations that will help in future to discern monophyletic subunits within *Remaneicaris*. We can mention the elongation of the dorsal urosomal windows to the lateral position, the splitting of the dorsal windows on urosomites 4 and 5 into lateral windows, the loss of the windows on the fourth urosomite, and the loss of the windows on the third urosomite.

Besides the two characters mentioned above, the inclusion of the new species in *Remaneicaris* is based on the overall similarity of the morphology of legs 2, 3 and 4 in the male and the position of leg 5. Unfortunately we do not know if the condition of these characters represents apomorphies for *Remaneicaris* or for a larger subgroup within the Parastenocarididae, as discussed below.

Leg 3 in the male consists of the coxa, the basis, and a 1-segmented exopod in the species described herein. The exopod is almost straight and the apophysis is short, rounded, and bears no setae (Figs. 4 C, 8 C). This specific condition of the apophysis is shared by most members of *Remaneicaris*, and is surely apomorphic in comparison with the condition present in several other parastenocaridids, in which the apophysis (which is homologous with a second exopodal segment) is rectangular and bears one or two setae (Rouch 1990, Glatzel 1991, Martínez Arbizu 1997).

The leg 4 endopod in the male is leaf-shaped and covered by many tiny cuticular spinules (Figs. 4 D, 8 D). This condition is apomorphic in comparison with the unmodified endopod present in the female (Fig. 5 B), which consists of 1 segment ornamented with a few strong spinules along

the outer margin, and no small and long spinules. Other *Remaneicaris* species seem to share this kind of endopod (Noodt 1962, 1963, 1965, 1972, Kiefer 1967), but published descriptions are not always detailed enough to use this character with confidence.

Leg 5 consists of a bilobed plate in both sexes. These plates are located medio-laterally on the ventral surface of the somite, far from each other and lacking an intercoxal sclerite. This is another apomorphic character present in both species described herein, in comparison with the mesially located leg 5 of, for instance, *P. hispanica*, the plates of which are jointed by a small intercoxal sclerite (Martínez Arbizu 1997). Unfortunately we do not know whether this is an apomorphy of *Remaneicaris*, or of a larger group within the Parastenocarididae.

A striking character of some species of *Remaneicaris* species is the presence of a 1-segmented endopod of leg 3 in the male. All other male parastenocaridids have lost this endopodal segment, retaining only a seta at this position, or even losing any remnant of the segment. This endopodal segment (armed with one seta) was described repeatedly by Noodt (1963, 1965, 1972), but it is absent in *R. oncophora* (Noodt, 1965), and *R. drepanophora* (Kiefer, 1967), where only a seta representing the endopod has been retained (Noodt 1965, Kiefer 1967). The presence of an endopod on the male leg 3 could not be verified with our new descriptions. Both species described here have one seta representing the endopod, but no endopodal segment. *Remaneicaris analuizae* n. sp. bears an additional hyaline structure on its inner margin, just above the endopodal seta (Fig. 4 C), while *R. euniceae* n. sp. has a protuberance proximal to the endopodal seta on the inner margin (Fig. 8 C). We do not believe, however, that Noodt may have misinterpreted homologues of these additional ornamentations with a true endopodal segment. The presence of an endopodal segment, if this is verified in the future, should be interpreted as a plesiomorphic character within Parastenocarididae. This would suggest a basal position of the genus within the family, because all

members assigned to the so called “Fontinalicaridinae” and “Parastenocaridinae” share the loss of the endopodal segment on male leg 3 (Schminke 1993).

Another peculiar symplesiomorphy of *Remaneicaris* is the presence of two setae on the proximal syncoxal endite of Mx2. Most members of the so called “Parastenocaridinae” and “Fontinalicaridinae” display only one seta at this endite. But two setae at this endite have been described for instance also for “fontinalicaridid” *Murunducaris* by Reid (1994) and the “parastenocarids” *P. brevipes*, *P. aethiopica* and *P. impervia* Cottarelli and Bruno 1995 (Reid 1995, Cottarelli and Bruno 1995). Remarkably two seta are also present in *Parastenocaris ahaggarica* Bozic, 1978 from Algeria (Bozic 1978), a species that resembles *Remaneicaris* in several respects and deserves redescription in order to confirm some unusual setation on Mx1 and leg 5. We prefer to not formally include *P. ahaggarica* into *Remaneicaris* awaiting its redescription.

Remaneicaris euniceae n. sp. differs from all other species of the genus known to date, in possessing a bilobed endopod of leg 2 in the male. The other species, *R. analuizae* n. sp., differs in the possession of an integumental window on the lateral margin of the fourth urosomite.

A hypothesis on the phylogenetic position of these new species within the genus *Remaneicaris* is difficult to form or evaluate without studying the type material of the known species. Therefore only some comparisons will be provided here.

Both new species have a row of spinules flanking the anal operculum. Similar ornamentation has been reported for *R. paraguayensis* (Noodt, 1963) and *R. remanei* (Noodt, 1963), both described from hyporheic groundwaters of Lake Ypacarai in Paraguay (Noodt 1963). But these spinules are much larger and stronger in the Paraguayan species. In addition, the Paraguayan species display a characteristic proximal constriction on the furcal ramus, a row of spinules on the dorsal margin of the fifth urosomite, an endopod on the male leg 3, and an almost triangular leg 5 with a large inner spine, all these characters differing from the conditions present in the Brazilian species.

Remaneicaris paraensis (Noodt, 1963) from the hyporheic of the Amazon River delta near Icoaraci, Pará, Brazil, also displays spinules flanking the operculum (Noodt 1963), and resembles the new species in having a bilobed leg 5. It can be distinguished from the new species in having an endopod on leg 3 in the male, and a row of long spinules on the proximal inner margin of the basis of leg 4 in the male. In addition to the species mentioned above, the only species of *Remaneicaris* known to possess spinules flanking the operculum are *R. divae* (Noodt, 1972) and *R. tageae* (Noodt, 1972) from the hyporheic zone of Cubatão River at the base of the Serra do Mar in the state of São Paulo, Brazil (Noodt 1972). The new species differ from *R. divae* in many respects, particularly the elongated furca, the elongated endopods of legs 2 and 4, and the elongated apophysis of the male leg 3 in *R. divae*. *Remaneicaris tageae* closely resembles both species described here, but can be distinguished by the absence of an additional proximal row of spinules on the dorsal margin of telson, which is present in both species from Minas Gerais.

In this contribution we advocate the use of the genus name *Remaneicaris* for those parastenocaridids belonging to a monophyletic group characterised by the displacement of the outer spine on the third exopod segment of leg 4 to a subterminal position. To our knowledge, 28 species display this character (Table 1). This list differs from the *Remaneicaris* concept of Jakobi (1972) by the inclusion of *R. hexacantha* (Kiefer, 1936) comb. nov. (as already suggested by Noodt 1963) known from the Rio Serido in Rio Grande do Norte, Brazil, and by the exclusion of 3 species (included by Jakobi in *Remaneicaris*) which do not display this character, viz. *P. dactyloides* Kiefer, 1967, *P. itica* Noodt, 1962, and *P. staheli* Menzel, 1916. These three species do not belong to *Remaneicaris*, and their phylogenetic relationships will be discussed elsewhere. Almost 50 % of all known South American parastenocaridid species belong to *Remaneicaris*.

The genus *Remaneicaris* is widely distributed in South America (Fig. 9). It has been reported from the Austral and the Holotropical biogeographic subregions of the Neotropis

(subregions according to Morrone 1996). From these facts we conclude that i) the genus was widely distributed in South America long before the elevation of the Andes, which began some 90 million years ago, and ii) that the sistergroup of *Remaneicaris* should be found within the former Gondwanaland but outside the Neotropis. Constructing a robust hypothesis of the phylogenetic relationships within *Remaneicaris* will be very useful for understanding the history of South American river basins. The present contribution is a first step towards that goal.

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Table 1: Known parastenocaridid species here ascribed to *Remaneicaris* and their occurrence in South and Central America (Fig. 9).

| Species | Location |
|---|----------|
| <i>R. palaciosi</i> (Noodt, 1962) | A |
| <i>R. meyerabichi</i> (Noodt, 1962) | A |
| <i>R. clandestina</i> (Noodt, 1963) | B |
| <i>R. drepanephora</i> (Kiefer, 1967) | B |
| <i>R. icoaraci</i> (Noodt, 1963) | C |
| <i>R. paraensis</i> (Noodt, 1963) | C |
| <i>R. hexacantha</i> (Kiefer, 1936) comb. nov. | D |
| <i>R. jujuyensi</i> (Noodt, 1965) | E |
| <i>R. paraguayensis</i> (Noodt, 1963) | F |
| <i>R. remanei</i> (Noodt, 1963) | F |
| <i>R. analuizae</i> Corgosinho and Martínez Arbizu n. sp. | G |
| <i>R. euniceae</i> Corgosinho and Martínez Arbizu n. sp. | G |
| <i>R. ignotus</i> (Dussart, 1983) | H |
| <i>R. divae</i> (Noodt, 1972) | I |
| <i>R. tageae</i> (Noodt, 1972) | I |
| <i>R. hurdi</i> (Jakobi and Silva, 1962) | J |
| <i>R. argentina</i> (Noodt, 1965) | K |
| <i>R. ciliata</i> (Noodt, 1965) | K |
| <i>R. cordobaensis</i> (Noodt, 1965) | K |
| <i>R. rhizophora</i> (Noodt, 1965) | K |
| <i>R. sierrae</i> (Noodt, 1965) | K |
| <i>R. membranacea</i> (Noodt, 1965) | L |
| <i>R. sanctiludovici</i> (Noodt, 1965) | L |
| <i>R. hecate</i> (Noodt, 1965) | M |
| <i>R. oncophora</i> (Noodt, 1965) | M |
| <i>R. persephone</i> (Noodt, 1965) | M |
| <i>R. pluto</i> (Noodt, 1965) | M |
| <i>R. psammae</i> (Rouch, 1962) | N |

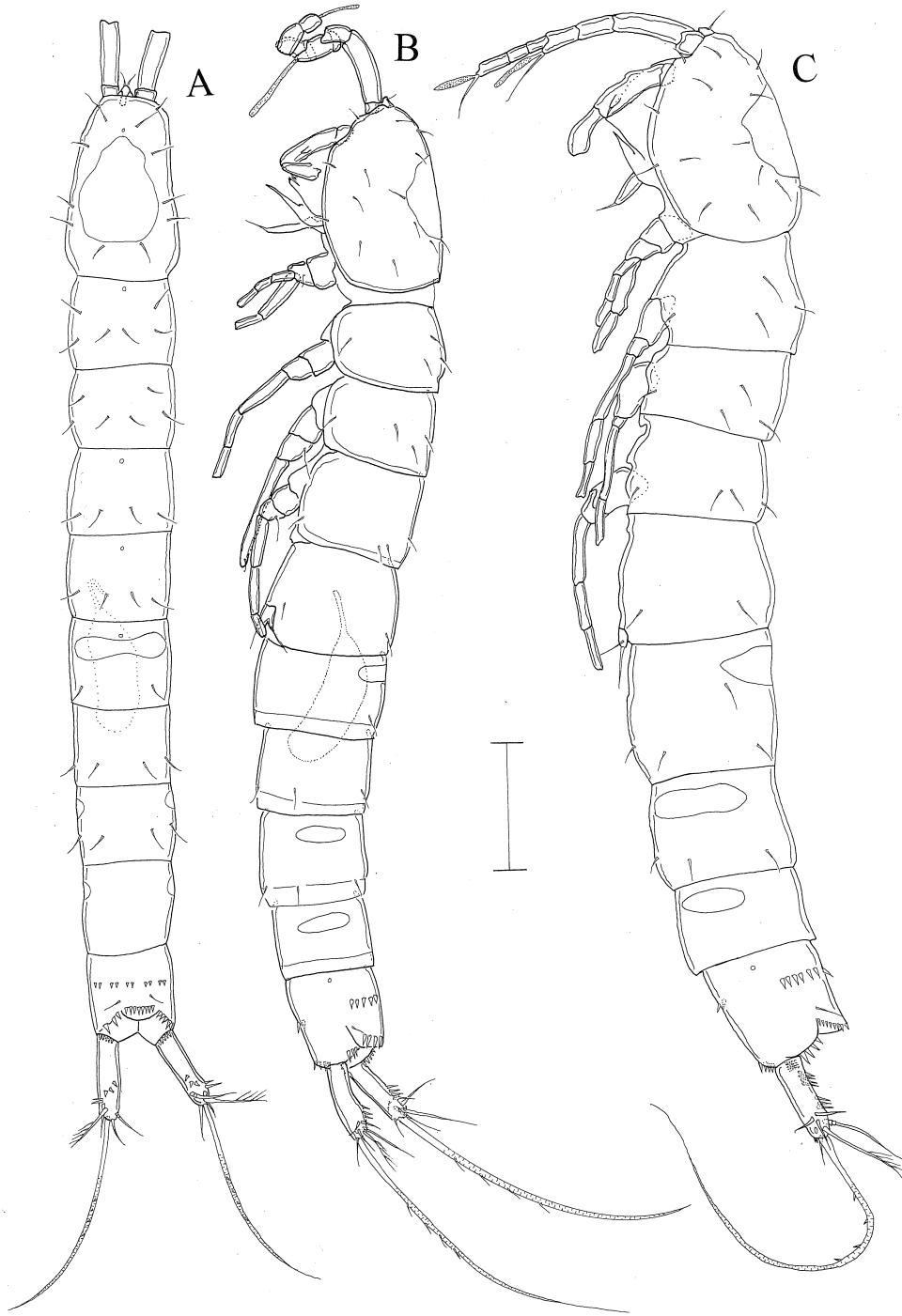


Fig. 1. *Remaneicaris analuizae* n. sp. A, habitus, dorsal view, male; B, habitus, lateral view, male; C, habitus, lateral view, female. Scale bar= 50 μ m.

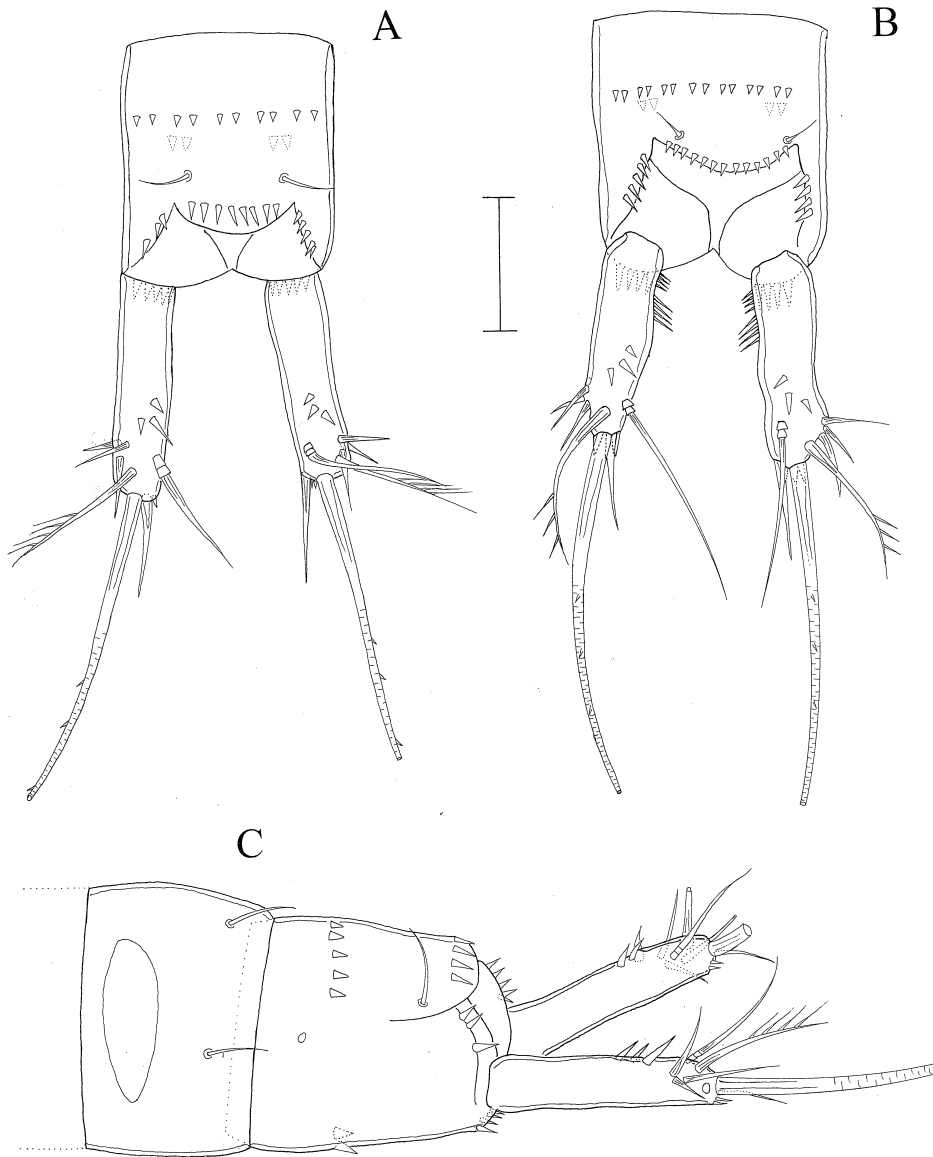


Fig. 2. *Remaneicaris analuizae* n. sp. A, telson, dorsal view, male; B, telson, dorsal view, female; C, fifth urosomite and telson, lateral view, male. Scale bar= 20 μ m.

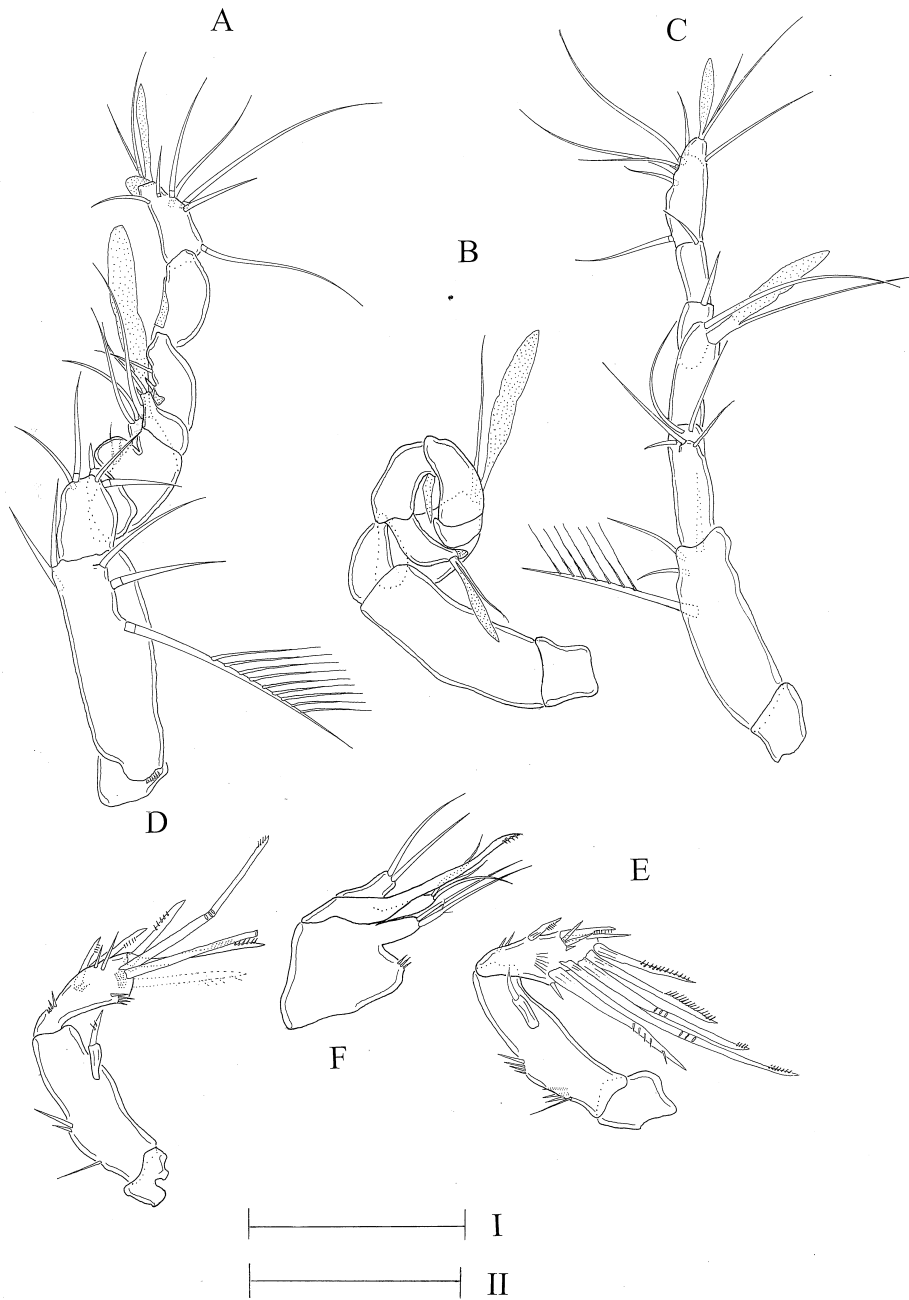


Fig. 3. *Remaneicaris analuizae* n. sp. A, male antennule; B, dorsal view of male antennule in grasping position; C, female antennule; D, male antenna; E, female antenna; F, Mx2 (Paratype). Scale bar A, B, C, D and E = 30 μ m, F = 20 μ m.

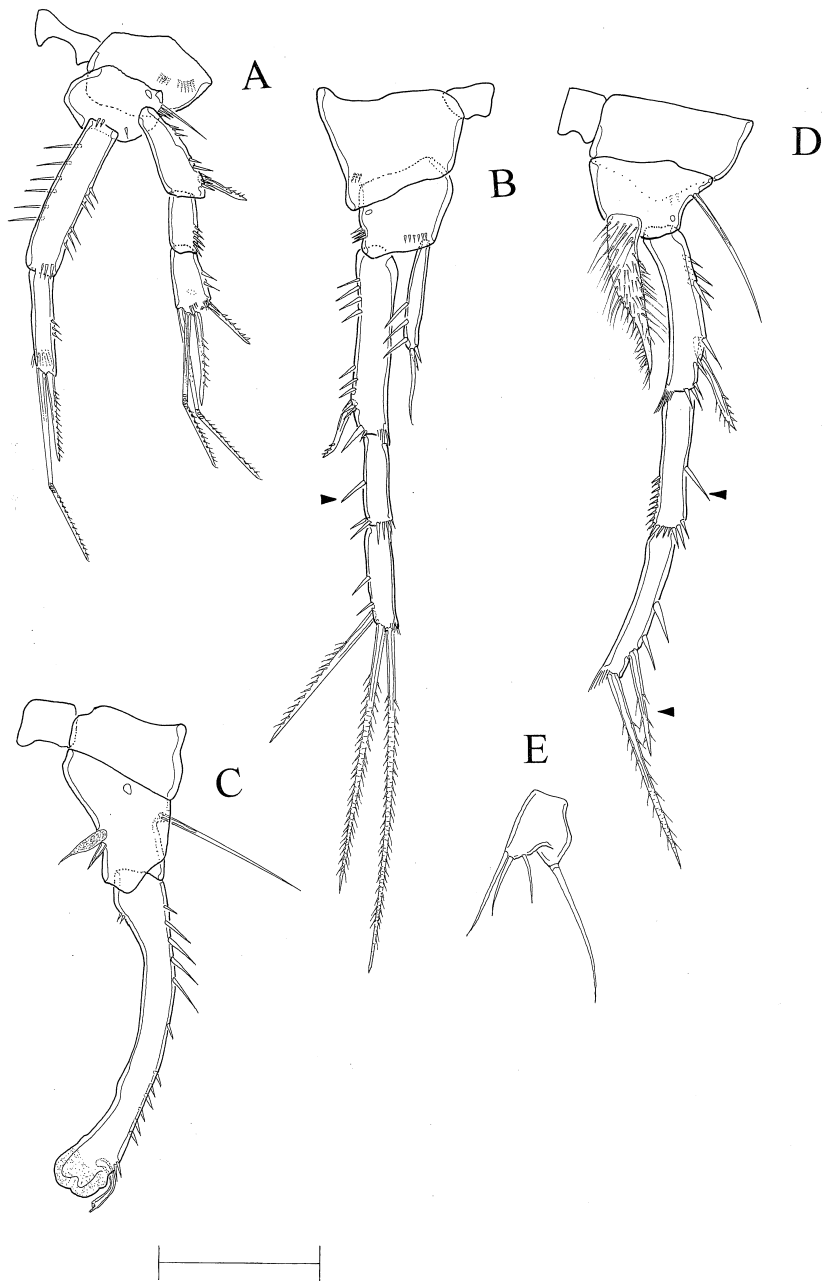


Fig. 4. *Remaneicaris analuizae* n. sp., male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, fifth thoracic somite with leg 5. Scale bar = 20 μ m.

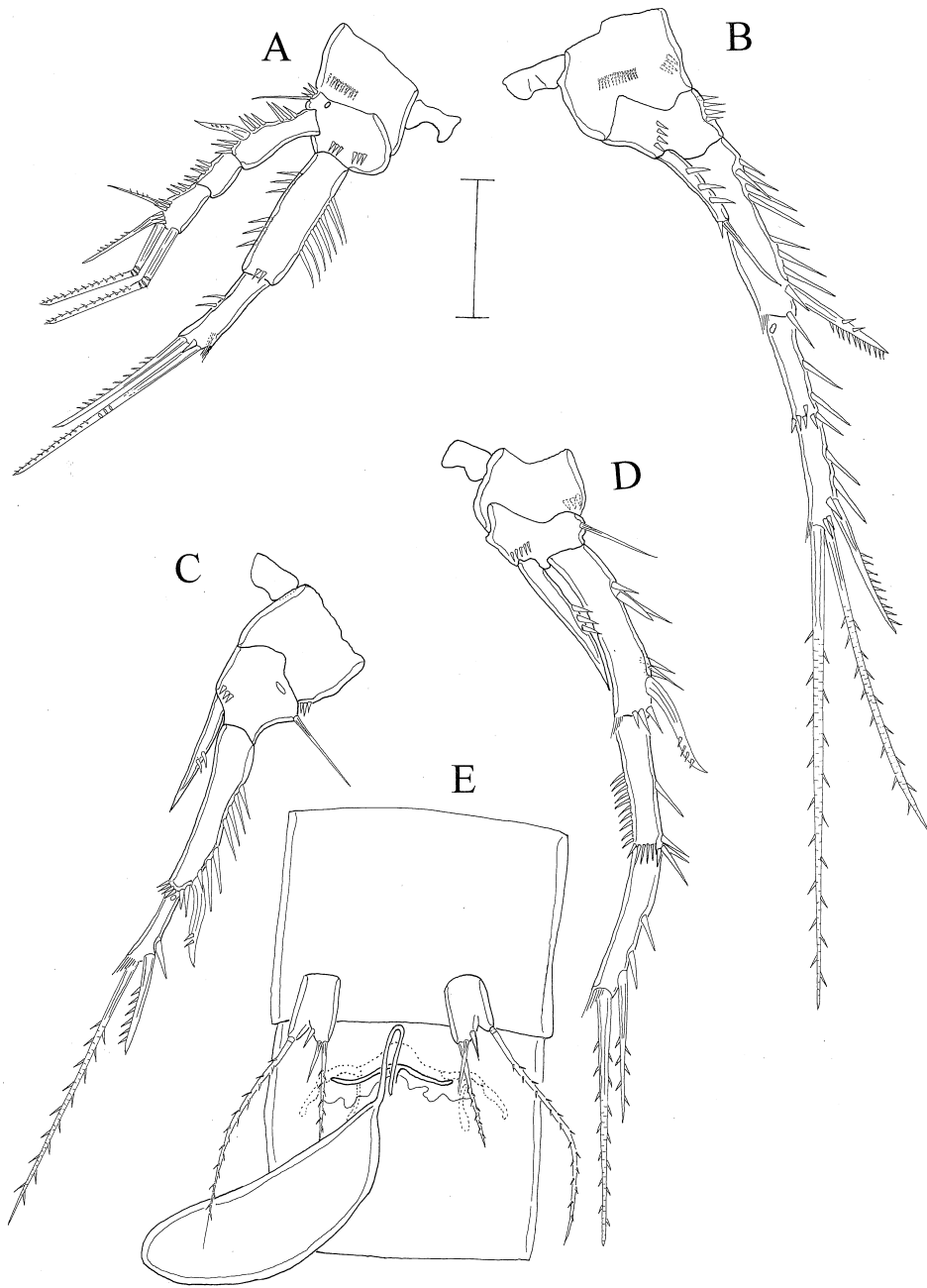


Fig. 5. *Remaneicaris analuizae* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, first urosomite with leg 5 and second urosomite with genital operculum and attached spermatophore. Scale bar =20 μ m

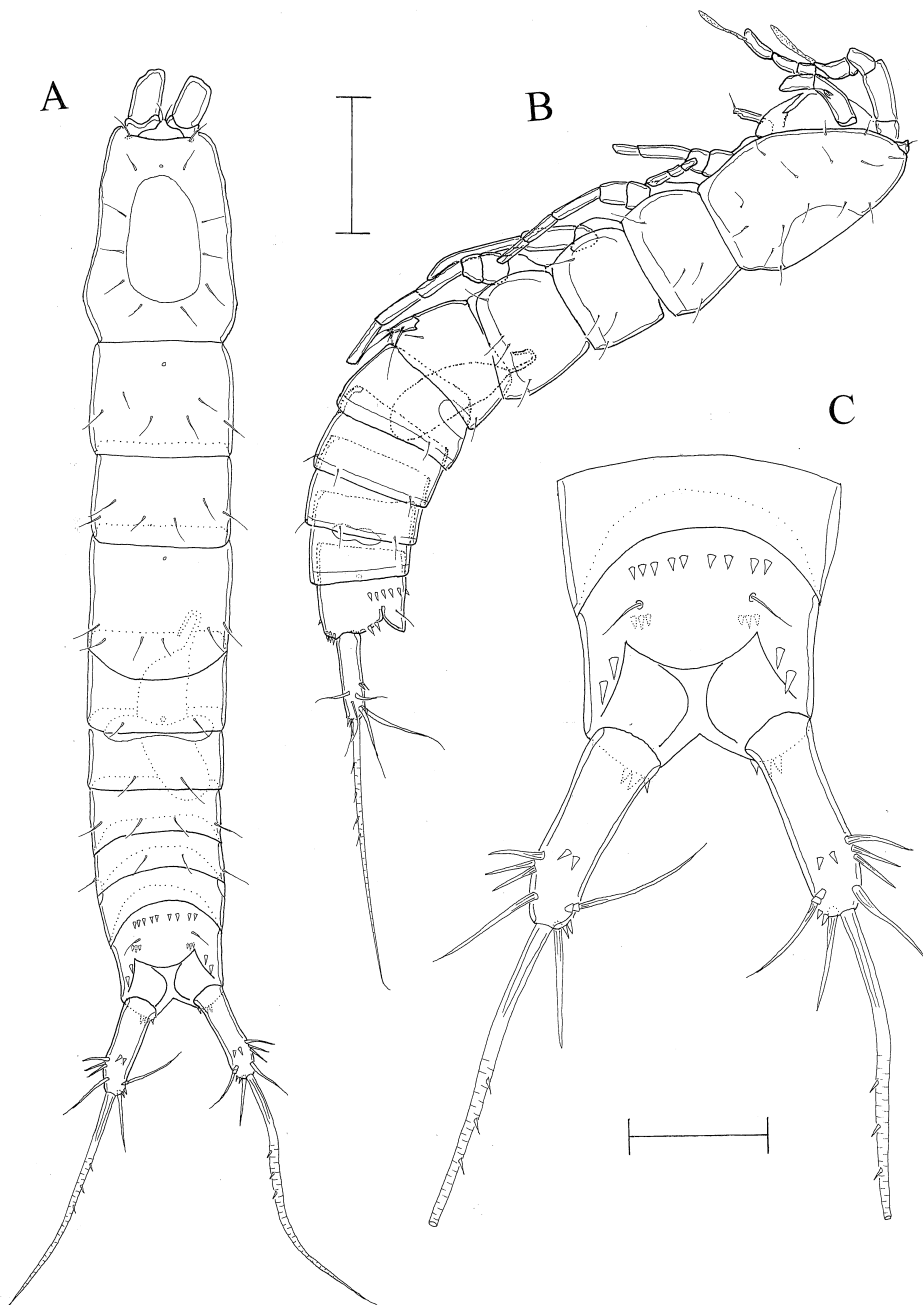


Fig. 6. *Remaneicaris euniceae* n. sp., male. A, habitus, dorsal view; B, habitus, lateral view; C, telson and fifth urosomal somite, dorsal view. Scale bars, A= 50 μ m, B= 20 μ m.

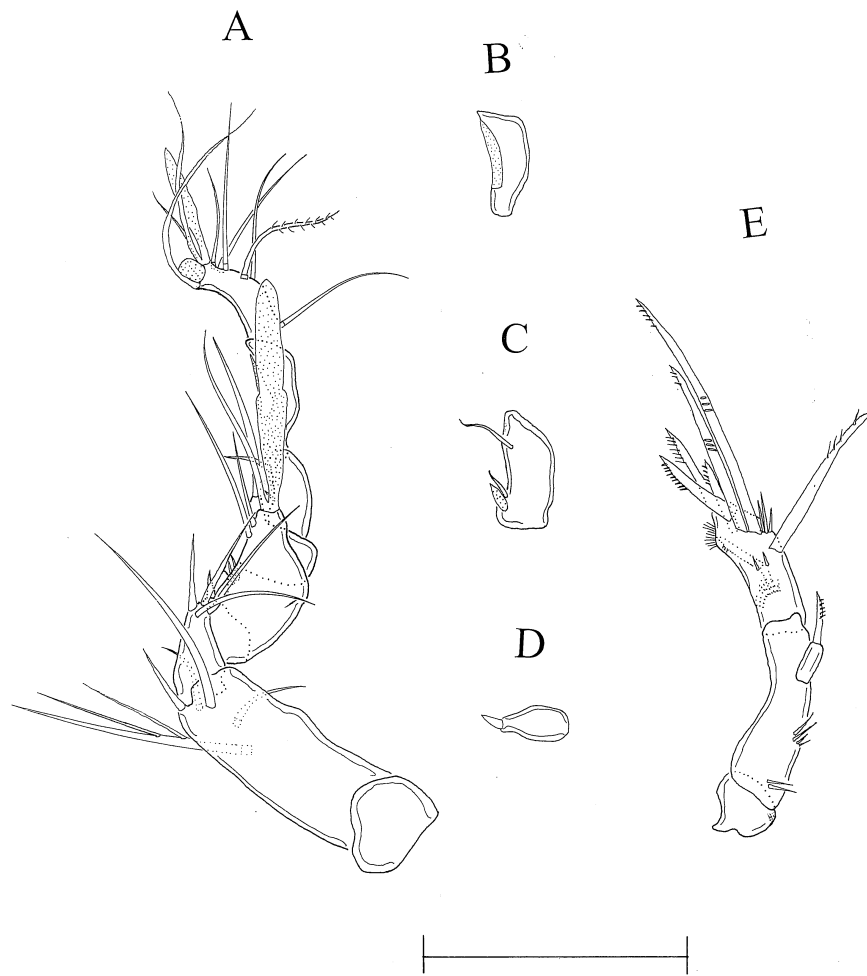


Fig. 7. *Remaneicaris euniceae* n. sp., A, male antennule; B, C and D, segments 8, 7 and 4 of male antennule respectively; E, male antenna. Scale bar =30 μ m.

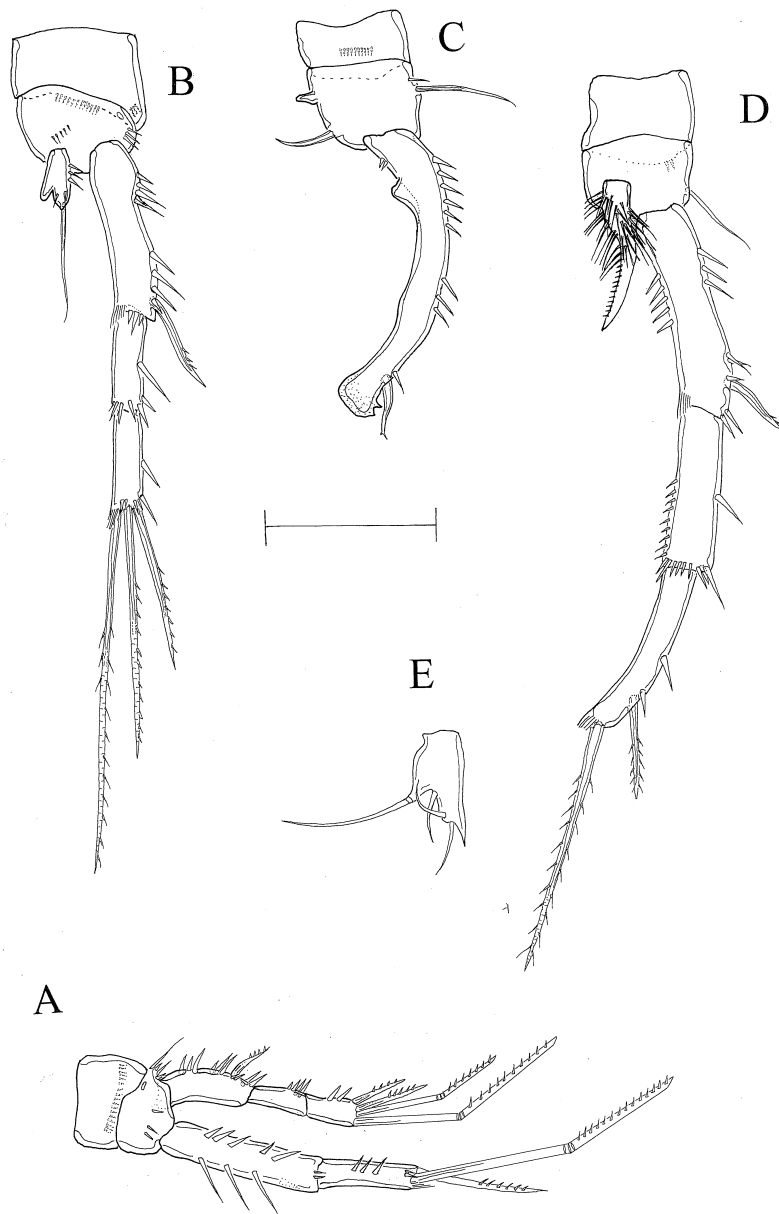


Fig. 8. *Remaneicaris euniceae* n. sp., male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar =20 μ m.

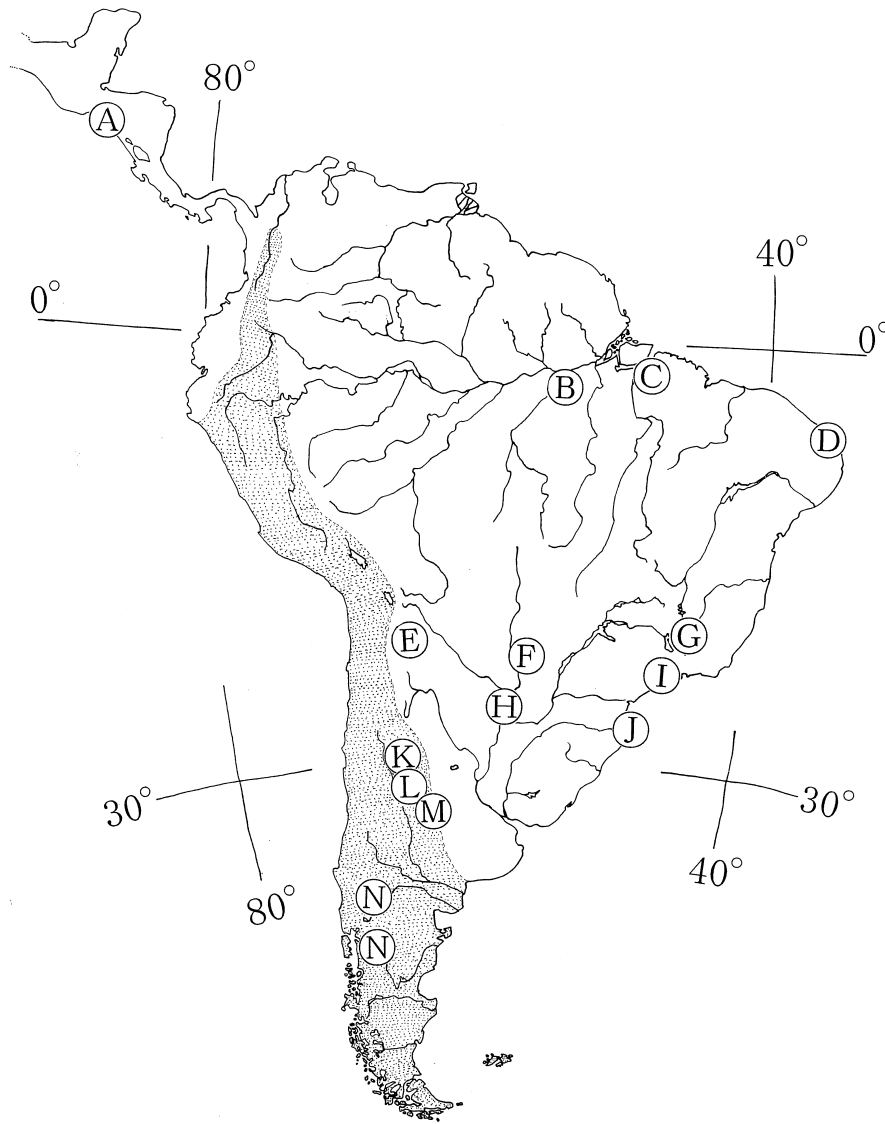


Fig 9. Map of South and Central America showing the locations where species assigned herein to *Remaneicaris* have been reported (see Table 1 for legends). Dotted area: Austral Subregion; clear area: Holotropical Subregion (subregions according to Morrone, 1996).

Chapter II

Three new species of *Remaneicaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro River, Minas Gerais, Brazil, with some remarks on the groundpattern of the Parastenocarididae

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Abstract

Three new species of the parastenocaridid genus *Remaneicaris* Jakobi, 1972 were discovered in interstitial near-shore waters of the small river Ribeirão do Ouro (a tributary of the Paraopeba river, in the São Francisco hydrographic basin). *Remaneicaris tridactyla* n. sp., *R. paratridactyla* n. sp. and *R. juliae* n. sp. are described in detail. The presence of a 1-segmented endopod on the male leg 3, previously reported for some *Remaneicaris* species, is confirmed here, and the phylogenetic relevance of this structure is discussed. The new species differ from each other by the shape of the leg 3 exopod and endopod, shape of leg 4 endopod, ornamentation of the telson and previous urosomites, and by the number of sensilla and dorsal pores. Some remarks on the groundpattern of the Parastenocarididae are given.

Keywords: Copepoda, Parastenocarididae, *Remaneicaris*, hyporheos, Neotropis, groundpattern.

1. Introduction

The family Parastenocarididae Chappuis, 1940 is a monophyletic group within Harpacticoida, being characterised and easily distinguished by the sexual dimorphism present in the third pair of legs. As an apomorphy, the males have these legs modified into a grasping organ (Martínez Arbizu and Moura 1994) that allows them to grasp the female during copulation (Glatzel 1991, 1996). In addition to the dimorphic third leg, the males present other diagnostic modifications, mainly in the endopod of the fourth leg and, sometimes, in the first, second, and fifth legs and the furca (Schminke 1991). These modifications constitute important characters used to distinguish species and supra-specific taxa.

The family currently contains 241 species and subspecies, but our knowledge of the phylogenetic relationships within the family is fragmentary. The monophyly of many genera proposed by Jakobi (1972) is still to be assessed. In South America, parastenocaridids encompass 66 known species, 33 of them reported from Brazil. These species belong to nine valid (see ICZN 2000 article 13) genera, viz. *Parastenocaris* Kessler, 1913; *Remaneicaris* Jakobi, 1972; *Brasilibathynellocaris* Jakobi, 1972; *Forficatocaris* Jakobi, 1969; *Pararemaneicaris* Jakobi, 1972; *Siolicaris* Jakobi, 1972; *Paraforficatocaris* Jakobi, 1972; *Potamocaris* Dussart, 1979 and *Murunducaris* Reid, 1994.

The genus *Remaneicaris* was proposed by Jakobi (1972) in order to accommodate the species included in the “remanei-group” (Noodt 1963) together with some other neotropical species described subsequently. The genus was revisited by Corgosinho and Martínez Arbizu (2005), who profoundly modified Jakobi’s concept in excluding some species from the genus, including some new and formerly known parastenocaridids in it, and by identifying some apomorphies which reveal its monophyletic status. *Remaneicaris* was considered valid by the former authors because it is

based on a valid type species, viz. *Remaneicaris remanei* (Noodt, 1963), and therefore article 13 of ICZN (2000) applies.

In this study we describe three additional, new species of *Remaneicaris* collected from the hyporheic zone of a small river in the São Francisco River basin, Minas Gerais, Brazil. The phylogenetic positions of the new species within the genus are discussed and some remarks on the groundpattern of Parastenocarididae are provided.

2. Material and Methods

The samples were taken on September 15 2000 next to the river bank of the Ribeirão do Ouro river, using the Karaman-Chappuis method (Chappuis 1942), washed through a 100 µm mesh, stained with rose bengal, and fixed with formalin at a final concentration of 4%. Animals were dissected in lactic acid and mounted on slides in glycerin. Drawings were made using a drawing tube (with a 2x lens) on a Leica DMR microscope, equipped with Normarski interference contrast, at 400 and 1000 magnification.

Abbreviations used are: A1 = antennule, A2 = antenna, Ae = aesthetasc, Md = mandible, Mx1 = maxillula, Mx2 = maxilla, Mxp = maxilliped, enp = endopod, exp = exopod, ARS = anterior row of spinules, PRS = posterior row of spinules, PES = pre-endopodal spinules, PEHZ = pre-endopodal hyaline zone, IBRS = inner basal row of spinules, RVS = row of “V” spinules, DESnl = distal exopodal spinule.

The term groundpattern is used in the same sense of the concept of Ax (1984) of Grundmuster.

The type material is deposited in the invertebrate collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

3. Descriptive part

Family Parastenocarididae Chappuis, 1940

Genus *Remaneicaris* Jakobi, 1972

Remaneicaris tridactyla n. sp.

Type material: Holotype, one dissected male on 7 slides (INPA 1339a).

Paratypes: One dissected female on 7 slides (INPA 1339c); 2 undissected males mounted on different slides (INPA 1339b and INPA 1339d), 1 dissected male mounted on 7 slides (INPA 1339e), 1 undissected female mounted on one slide (INPA 1339f).

Derivatio nominis: The species name refers to the trifold structure of the modified thumb of the male leg 3.

Locus typicus: Ribeirão do Ouro river, Sítio do Corgosinho, Florestal, state of Minas Gerais, Brazil.

Coordinates: 19°48'19S, 44°27'45W.

Male habitus (Fig. 1 A-B). Length 404 μm (measured from the tip of rostrum to the posterior rim of anal operculum). Rostrum not fused to cephalothorax, with a wide base and two sensilla on the tip. Cephalothorax and second urosomite with 1 dorsal integumental window. Urosomite 5 with a pair of lateral integumental windows. Dorsal pores on cephalothorax, thoracic somites 1 and 3 and second urosomite. Telson with 1 pair of lateral pores. For sensilla on tergites see Fig. 1 A-B. Telson with 1 dorsal row of 10 spinules located on the anterior third (ARS), 2 rows of 5 large spinules on the posterior half (PRS), anterior to the sensilla, not reaching the operculum and 2 ventral rows of large spinules on the posterior half, near the insertion of the furca (Fig. 2 A-B). Anal operculum smooth and quadratic. Furca (Figs. 1 A-B and 2 A-B) about 6 times as long as wide, with 7 setae. All setae located on the posterior third. A1 (Fig. 3A) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae, 1 modified seta on the last segment (indicated by

an arrow) and 1 hyaline spinule on the seventh and eighth segments. A2 (Fig. 3 B) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing an anterior hyaline frill and 7 setae. Md, Mx1, and Mxp armature as *P. hispanica* Martínez Arbizu 1997; Mx2 with 2 slender setae on the proximal endite and 3 on the distal endite, as in *R. analuizae* Corgosinho and Martínez Arbizu, 2005. Leg 1 (Fig. 4 A) coxa without setae or spines, with 2 rows of spinules on the posterior side; basis with outer seta and 1 pore on the anterior side, 3 spinules on the outer margin, and 3 distal spinules anterior to the insertion of the enp; enp and exp of the same size; enp 2-segmented, segment 1 with 1 row of 5 long spinules along the inner margin, 1 row of 4 spinules on the outer margin and a posterior hyaline frill; segment 2 with a posterior hyaline frill and 2 distal setae, 1 of them geniculated; first enp segment of the same size of the first two exopodites; exp 3-segmented, segment 1 with 1 outer spine, segment 2 without setae or spines, segment 3 with 2 outer spines, 2 geniculated setae and a posterior pore. Leg 2 (Fig. 4 B) coxa without setae or spines, with 1 row of small spinules and 3 outer spinules on the posterior side; basis without outer seta and ornamented with 1 row of spinules on the outer margin, 1 row of small spinules at the level of the enp insertion and 1 pore near the outer margin; exp 3-segmented, the first segment approximately the same length as the remaining exopodites, with a proximal row of spinules on the outer margin, distributed in a “V”, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill, segment 2 without armature, with 2 spinules located mesially on the outer margin and with a row of distal spinules, segment 3 with 3 setae, a distal hyaline frill on the inner corner and 2 spinules located mesially on the outer margin; enp 1-segmented with 1 distal seta, 2 distal spinules, and 3 spinules along the outer margin. Leg 3 (Fig. 4 C-D) coxa without setae or spines; basis with an outer seta; enp 1-segmented with 3 subdistal spinules; exp 1-segmented, elongated, bearing 2 rows of spinules along the outer margin and with 1 very modified seta (“thumb”) in a subdistal position. Leg 4 (Fig. 4 E) coxa without setae or spines, with 3 small spinules on the posterior side; basis with outer seta,

1 pore near the outer margin, a row of spinules on the inner margin (IBRS) and 1 row of larger spinules near the insertion of the enp (PERS), in a hyaline area of the basis (PEHZ); exp 3-segmented, segment 1 almost same length as remaining segments, with an outer spine, a proximal row of spinules distributed in a “V” shape (RVS) on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill on the distal corner, segment 2 without setae, with a row of spinules on the distal portion, a row of small spinules along the inner margin, conferring on it a serrated shape, and with 2 long spinules located mesially on the outer margin, segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner corner and 3 spinules located mesially on the outer margin; enp 1-segmented, leaf-shaped, covered with numerous long spinules (hirsute) along the inner and outer margin and with a distal spine. Leg 5 (Fig. 2 C) triangular, ending in a spiniform process and with all setae arranged on the outer margin.

Female: Sexually dimorphic in number of body segments, A1, leg 3, leg 4 and genital field.

Habitus (Fig. 5 A-B). Length 413 μm (from the tip of rostrum to posterior rim of telson). Rostrum as in male. Cephalothorax and genital double-somite with 1 dorsal integumental window. Urosomite 4 with 1 pair of lateral integumental windows. Dorsal pores as in male and 1 pair of lateral pores on the telson. For sensilla on tergites see Fig. 5 A-B. Telson with 2 dorsal rows of 4 spinules on the anterior third (ARS), 2 rows of 4 larger spinules on the posterior half, not reaching the operculum (PRS) and 2 ventral rows of large spinules on the posterior half, near the insertion of the furca (Fig. 5 A-B and 6 A-B). Anal operculum smooth and convex (Fig. 6 B). Furca (Fig. 6 A-B) about 5 times as long as wide, with 7 setae. All setae located on the distal third, as in males. A1 (Fig. 7A) 7-segmented; number of setae beginning with proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 (Fig. 7B) with allobasis, 1-segmented exp with 1 seta, 1-segmented enp bearing 7 setae and a posterior hyaline frill. Buccal parts as in male. Leg 1 (Fig. 7 C) coxa without setae or spines and with 1

posterior row of spinules; basis with outer seta, 3 outer accessory spinules and 3 distal spinules near the insertion of enp; enp and exp as in males. Leg 2 (Fig. 7D) as in males. Leg 3 (Fig. 7E) coxa without setae or spines, with 2 rows of spinules on the posterior side; basis with 1 outer seta, and ornamented with 1 row of spinules near the insertion of the enp; exp 2-segmented, segment 1 with an outer spine, a proximal row of spinules and a row of spinules next to the outer spine, segment 2 with 1 spine, 1 seta and 2 long spinules on the outer margin; enp 1-segmented and spiniform, with 2 spinules on the outer margin and 1 spinule on the inner margin. Leg 4 (Fig. 7F) as in males, except for the presence of a spiniform enp ornamented with 1 row of 4 spinules on the outer margin and a row of small spinules on the basis, near the insertion of the enp. Leg 5 (Fig. 6C) as in male. Genital field as illustrated in Fig. 6C, with a single, mesially located copulatory pore. Gonopore is a transverse slit.

***Remaneicaris paratridactyla* n. sp.**

Type material. Holotype, 1 male, dissected and mounted on 7 slides (INPA 1391a-g).

Paratypes: 1 dissected female mounted on 7 slides (INPA 1392a-g), 1 male mounted on 9 slides (INPA 1393a-i), 1 undissected male (INPA 1394a) and 1 female (INPA 1394b) mounted on one slide each other.

Derivatio nominis: The species name refers to the complex structure of the modified thumb of leg 3, somewhat similar to the homologous structure found in *R. tridactyla* n. sp.

Locus typicus: Ribeirão do Ouro river, Sítio do Corgosinho; Florestal, state of Minas Gerais, Brazil.

Coordinates: 19°48'19S, 44°27'45W.

Male habitus (Fig 8 A-B). Length 413 µm (from the tip of rostrum to posterior rim of telson).

Rostrum with wide base and 2 sensilla on tip. Cephalothorax and second urosomite each with 1

dorsal integumental window. Urosomite 5 with lateral integumental window. Dorsal pores on cephalothorax, thoracic somites 1 and 3 and second urosomite. One pair of lateral pores on telson. Arrangement of sensilla on tergites illustrated in Figs. 8 (A-B). Telson (Fig. 9 A-B) with a dorsal row of 8 spinules on the anterior half (ARS) and 2 rows of 3 spinules on the posterior half (PRS), near the operculum; ventrally, with a row of 4 spinules near the insertion of the furca. Anal operculum quadratic, without spinules. Furca 3.5 times longer than wide, with 7 setae, all located on distal third. A1 (Figs. 10A) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae, last segment with 1 modified seta as in *R. tridactyla* n. sp. A2 (Fig. 10B) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp with 7 setae. Mouthparts armature as *R. tridactyla* n. sp.; leg 1, leg 2 and leg 4 (Fig. 11A, B and E) similar to the respective appendices of *R. tridactyla* n. sp. male. Leg 3 (Fig. 11 C and D) coxa without setae or spines, with 2 rows of spinules on the posterior side; basis with outer seta; enp 1-segmented with 1 terminal seta; exp 1-segmented, elongate, bearing 2 rows of spinules along outer margin; subdistally, with 1 very modified seta (thumb). Leg 5 (Fig. 10 C) triangular, ending in a spinulose process and with all setae located on the outer margin.

Female: Sexually dimorphic in number of body segments, A1, leg 3, leg 4 and genital field.

Habitus (Fig. 12 A-B). Length 456 μm (from rostrum to operculum). For pores and sensilla see Fig. 12 A and B. Telson (Fig. 12 A-B) with a dorsal row of 9 spinules on the anterior half (ARS) and 2 rows of 3-4 spinules on the posterior half (PRS) near the operculum; ventrally, with a row of 4 spinules near the insertion of the furca. Operculum quadratic, without spinules. Furca 4 times longer than wide, with 7 setae, all located on distal third. A1 and A2 (Fig. 13 A-B), mouthparts, leg 1, leg 2, leg 3, leg 4 and genital field (Fig. 14 A-E) are similar to the respective structures of females of *R. tridactyla* n. sp., but with some differences in the ornamentation of the basis of legs 1 to leg 4.

***Remaneicaris juliae* n. sp.**

Type material. Holotype, 1 male, dissected and mounted on 5 slides (INPA 1340a-e). The slide with the A1, A2 and mouthparts was lost.

Paratypes: 1 dissected female mounted on 7 slides (INPA 1341a-g), 1 partially dissected male mounted on 1 slide (INPA 1342a) and 1 undissected female mounted on 1 slide (INPA 1342b).

Derivatio nominis: The species name honors a friend, Julia Funk, of Freiburg, Germany.

Locus typicus: Ribeirão do Ouro river, Sítio do Corgosinho; Florestal, state of Minas Gerais, Brazil.

Coordinates: 19°48'19S, 44°27'45W.

Male habitus (Fig 15 A-B). Length 441 μ m (from rostrum to operculum). Rostrum with wide base and 2 sensilla on tip. Cephalothorax and second urosomite each with 1 dorsal integumental window. Urosomite 5 with 1 pair of lateral integumental windows. Dorsal pores on cephalothorax, thoracic somites 1 and 3 and second urosomite. One pair of lateral pores on telson. Arrangement of sensilla on tergites illustrated in Figs. 15 (A-B). Urosomites 4 and 5 with a posterior row of large spinules (Fig. 16B). Telson (Fig. 16 B-C) with a dorsal row of 8 spinules on the anterior half (ARS) and 2 rows of 3 spinules on the posterior half (PRS) near the operculum; ventrally, with a row of 4 spinules near the insertion of the furca. Operculum quadratic, without spinules. Furca 3.5 times longer than wide, with 7 setae, all of them located on distal third. A1 (Figs. 17 A) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae, as in the former species, with a modified seta on the last segment. A2 as in the previously described species, with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp with 7 setae; Mouthparts armature as in *R. tridactyla* n. sp.. Leg 1, leg 2 and leg 4 (Fig. 17 B, C and E) similar to the respective appendices found in males of *R. tridactyla* n. sp. and *R. paratridactyla* n. sp., with the exception of

the end of leg 4, somewhat more blunt and with a blade-shaped distal spine. Leg 3 (Fig. 17 D) coxa without setae or spines; basis with outer seta, 2 outer spinules and 1 proximal row of spinules; endopod 1-segmented, without any armature or ornamentation; exopod 1-segmented, elongated, bearing 1 row of spinules along outer margin; subdistally, with 2 strong spinules and a strong and curved spine. Leg 5 (Fig. 16A) triangular, ending in a spinulose process and with all setae located on the outer margin.

Female- No striking differences in armature and ornamentation between appendages of the female of *R. juliae* n. sp. and the previously described species. Sensilla and pore patterns just as in males, with the exception of the genital double-somite which carries 4 setae. Telson and previous 2 urosomites as in males.

4. Discussion

The three species described here share the subdistal position of the outer spine on the third exopodal segment of leg 4, a character that has been considered as the most important synapomorphy of *Remaneicaris* (Corgosinho and Martínez Arbizu, 2005).

Remaneicaris tridactyla n. sp., *R. paratridentata* n. sp. and *R. juliae* n. sp. share the presence of a posterior row of spinules (PRS, arrowed in Fig. 2A) on the dorsal margin of the telson, located directly anterior to the sensilla; as well as a second row of spinules located anteriorly on the dorsal margin of the telson (ARS, arrowed in Fig. 2A). These species also share the presence of a row of up to 5 strong spinules located ventrally near the insertion of the furca. These characters are present also in *R. remanei* (Noodt, 1963) and *R. paraguayensis* (Noodt, 1963), and can be used to define a monophyletic group within the genus. *Remaneicaris paraensis* (Noodt, 1963) and *R. hexacantha* (Kiefer, 1936) display the PRS and the ventral row of spinules, but lack the ARS. Other species such

as *R. persephone* (Noodt, 1965) and *R. sierrae* (Noodt, 1965) display the PRS, but other characters indicate that these species belong to another monophyletic subgroup within *Remaneicaris*. For instance *R. persephone* and *R. sierrae* belong to a larger group that shares the presence of a leg 6 with 2 setae in females. No seta on leg 6 is present in the monophyletic group formed by *R. tridactyla* n. sp. and the other species around it. Although the presence of armature elements on leg 6 may be considered a plesiomorphic condition compared to the lack of them, we believe that the most parsimonious assumption is to consider the appearance of these elements as a synapomorphy for a more derived group within *Remaneicaris*, since the alternative, considering it as a plesiomorphy, would imply the loss of this character at least four times within the genus. Remarkably no armature elements on leg 6 are known for any other species within Parastenocarididae. Within this group, *R. persephone* is more closely related to *R. hecate* (Noodt, 1965), with which it shares the elongation of enp of leg 4 in the females, passing the distal rim of first exp segment, as a synapomorphic character. *Remaneicaris sierrae* is most closely related to *R. cordobaensis* (Noodt, 1965) and *R. ciliata* (Noodt, 1965), sharing the loss of a row of large spinules (PERS) near the insertion of leg 4 enp in males as a synapomorphy. The phylogenetic position of *R. hexacantha* is difficult to assess because males are unknown; but it seems that this species is closely related to the species around *R. tridactyla* n. sp., *R. paratractactyla* and *R. juliae* n. sp. A ARS is present in *R. analuizae* Corgosinho and Martínez Arbizu, 2005 and *R. euniceae* Corgosinho and Martínez Arbizu, 2005. but these species belong to a different monophyletic subgroup within *Remaneicaris*, sharing the development of a hyaline structure on the distal rim of the last antennular segment in males.

R. tridactyla n. sp. differs from all other species of the genus by the complex structure of the “thumb”, which is divided into three processes (Fig. 4 C and D). Within *Remaneicaris*, this condition is only present in *R. paratractactyla* n. sp., although this structure is not so strongly

developed in the latter species (Fig. 11 C and D). To our knowledge, no other species of Parastenocarididae display this structure. The illustrations by Noodt (1962, 1963, 1965) and Kiefer (1967) of the leg 3 of the males of *R. palaciosi* (Noodt, 1962), *R. clandestina* (Noodt, 1963), *R. argentina* (Noodt, 1965), *R. jujuyensis* (Noodt, 1962) and *R. drepanephora* (Kiefer, 1967) suggest a similar condition in these species. However, study of the type material revealed that they are not homologous to the condition present in *R. tridactyla* n. sp. but is formed by the transformation of the distal spinule (DESnl) on the outer margin of the exp, together with the elongation of the outer setae (thumb) (arrowed in Fig. 18). *Remaneicaris juliae* n. sp. has to be considered more primitive, because it does not have the trifold thumb (Fig. 17 D). It differs from the other species by the presence of a row of strong spinules on the fourth and fifth urosomites (Fig. 15 A and B, Fig. 16 B).

The three species described above have a lateral integumental window on the fifth urosomite of the male (fourth urosomite in the female). This character is present in almost all *Remaneicaris* species. Other, alternative patterns can be seen within the genus. For example, *Remaneicaris analuizae* Corgosinho and Martínez Arbizu, 2005 has a second lateral window on the fourth urosomite in the male (third urosomite in the female). *Remaneicaris palaciosi* and *R. meyerabichi* (Noodt, 1962) have a window on the last urosomite, which extends from the dorsal to the lateral margin (Noodt 1962). Other, undescribed species have come to our knowledge that have on the fifth male urosomite and fourth female urosomite, two windows on each side laterally, which seems to be the result of a split of the previously single lateral window. Finally, observations of Noodt's type material revealed that in *R. hecate*, *R. pluto* (Noodt, 1965) and *R. persephone* and in females of *R. oncophora* (Noodt, 1965), the integumental window of the second urosomite is divided into two, latero-dorsal windows. It seems that *Remaneicaris ignotus* (Dussart, 1983) is the most basal species within the genus (Corgosinho and Martínez Arbizu in press; Corgosinho 2007) and it does not have lateral windows, but rather one dorsal window on each of urosomites 2-5.

4.1. Remarks on the groundpattern of Parastenocarididae

Species of the genus *Remaneicaris* have many plesiomorphic characters, which allow us to make some remarks on the reconstruction of the groundpattern of the family.

4.1.1. Integumental windows

Besides *Remaneicaris*, only some African Parastenocarididae, viz. *P. caffer* Chappuis, 1936; *P. madagascarensis*, Chappuis, 1952; *P. forficulata* Chappuis, 1952; *P. arenosus* Fryer, 1956 and *P. aethiopica* Cottarelli and Bruno, 1995 display lateral or ventro-lateral windows on the fourth urosomite of females and fifth urosomites of males (Chappuis 1936, 1952; Fryer 1956; Cottarelli and Bruno 1995). We do not share the idea that this can be used as a synapomorphy to unify all these species together in a monophyletic, suprageneric group (Corgosinho and Martínez Arbizu 2005). Since *Remaneicaris* does not have the lateral position of integumental windows in its groundpattern (see *R. ignotus*), the appearance of lateral windows on the African species should be interpreted as a homoplasy. The exclusion of *R. palaciosi* and *R. meyerabichi* from the *remanei*-group (*Remaneicaris*) based on the presence of dorsal integumental windows (Reid 1994), is not accepted here because the displacement of the integumental windows to a lateral position occurs within *Remaneicaris* and is therefore not a diagnostic synapomorphy for the genus.

4.1.2. Cuticular pores and sensilla

Males and females of *R. tridactyla* n. sp. and *R. juliae* n. sp., and males of *R. paratridactyla* n. sp. share a pattern of cuticular pores. They have 1 dorsal pore on the cephalothorax, 1 dorsal pore on the first and third thoracic somites and 1 dorsal pore on the second urosomite (genital double-somite in females) (Fig. 5). The telson has one lateral pore on each side. Females of *R.*

paratridactyla n. sp. have one additional dorsal pore on the last urosomite (Fig. 12). Illustrations by Ahnert (1994) of species of *Potamocaris* and *Forficatocaris* give the position of dorsal pores on the thorax and urosomites, and Martínez Arbizu (1997) showed the position of these pores in *P. hispanica*. The comparison of these drawings with our observations and considering three other undescribed species of *Remaneicaris* allows us to say that the groundpattern for the family is, probably, the presence of one dorsal pore on each somite and one lateral pore on each side of the telson.

The study of the sensilla patterns within the Parastenocarididae has been neglected by previous authors working with these animals, probably because the number and position of these structures is difficult to discern accurately. Almost nothing is known about the sensilla patterns even within the Harpacticoida, but it seems that the number and position of these structures can provide interesting phylogenetic information. The maximum number of sensilla described until now for a species of Parastenocarididae in males is 17/6/6/5/5/4/4/5/0/1 (Ahnert 1994), counted from cephalothorax to telson, considering only one of the lateral sides of the animal. It is very difficult at present to say anything about the groundpattern of this character, and more accurate observations of other Parastenocarididae are needed. The pattern of sensilla in males of *R. tridactyla* n. sp. is 14/5/4/4/4/1/3/3/0/1, for *R. paratridactyla* n. sp. is 14/5/5/4/3/2/3/3/0/1 and for *R. juliae* n. sp. is 14/4/4/4/3/2/3/3/0/1. The pattern in *Remaneicaris* females is the same, with the exception of the double-somite which carries 4 sensilla. One of them, near the dorsal integumental window, probably is homologous to the dorsal sensilla present on the second urosomite of males (arrowed and signaled as “h” in Fig. 1 and 5).

Interestingly, it seems that no members of Harpacticoida (perhaps even no copepod) have sensilla on the somite anterior to the telson.

4.1.3. Mouthparts

The mouthparts seem to be very conservative within the family, although some important differences can be seen in some groups. The Md, Mx1 and Mxp are quite similar and small differences do not involve changes in number of setae and spines. The groundpattern of the family as present in *Remaneicaris* is as follows: Mandible with a coxal gnathobasis bearing 1 seta and a palp with 2 setae; Mx1 with precoxal arthrite with 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines and 1 slender seta), coxa with 1 seta and basis with 3 setae, and Mxp 3-segmented, distal segment with 1 claw-like seta. The Mx1 condition described for *P. ahaggarica* Bozic 1978 having a precoxal arthrite with more than 3 spines, coxa with 2 setae, enp with 2 setae and exp represented by 1 seta deserves re-examination, because it represents a dramatic deviation from the pattern observed in all other species of the family. Reid (1995), while redescribing *P. brevipes* Kessler, 1913 stated that the Mx1 of this species is “like that of *P. ahaggarica*”. Our own examination of *P. brevipes* from Germany showed that the segmentation and setation of Mx1 is the same as in other Parastenocarididae and not like *P. ahaggarica* as depicted by Bozic (1978). The presence of 8 setae on the precoxal arthrite of *Simplicaris lethae* Galassi and De Laurentiis, 2004 and 7 on *Potamocaris bidens* Noodt, 1955 and *Forficatocaris* spp. (Ahnert 1994), deserves re-confirmation because we have never observed this number of elements in other parastenocaridids, or even in species belonging to the *Potamocaris-Forficatocaris* complex collected by us in Brazil.

Another, peculiar symplesiomorphy of *Remaneicaris* is the presence of 2 setae on the proximal syncoxal endite of Mx2 (all other parastenocaridids have only 1 seta) and 3 bare setae on the distal endite (one of them pinnated in all parastenocaridids but *Remaneicaris*). Two setae on the proximal syncoxal endite have been described for *Murunducaris*, *P. brevipes* and *P. ahaggarica*. Re-examination of the type species of *Murunducaris* as well as of *P. brevipes* from Germany revealed

that only 1 seta instead of 2 is present on this endite in these species also. The pattern in *P. ahaggarica* requires re-confirmation (see above).

4.1.4. Antennule

Remaneicaris species have a 9-segmented A1 in the male. The same number of segments occurs also in other parastenocaridids such as *Potamocaris* (Martínez Arbizu in prep). The groundpattern of A1 in Parastenocarididae can be reconstructed as a 9-segmented antennule, with the following armature: 0/5/4/2/5+Ae/1/3?/2/9+Ae. Probably representing the following ancestral segments (sensu Huys and Boxshall 2001): I; II-VIII; IX-XII; XIII; XIV-XVI; XVII-XVIII; XIX-XX; XXI-XXII; XXIII-XXVIII. The 8-segmented condition in some genera and species such as *Murunducaris* (personal observations), *Brasilibathynellocaris* (personal observations), *P. trichelata* Reid, 1994, *P. hispanica* and *Simplicaris* Galassi and De Laurentiis, 2004 should be interpreted as a derived condition, being the result of the non-formation of segment 6. All *Forficatocaris* species studied by Ahnert (1994) display an 8-segmented antennule also. However, in his drawings, the third and fourth segments of the groundpattern of Parastenocarididae are represented by a single segment carrying 6 setae. After re-examination of Noodt's type specimens, we concluded that segments 3 and 4 are separated in these species also. Groundpattern segment 4 is very small and difficult to discern without good optics, which may be the reason that this segment has been rarely illustrated by parastenocaridid researchers in the past. The 10-segmented condition described for the male of *Potamocaris estevesi* Reid, 1991 (Rocha *et al.* 1998) is probably wrong. The female antennule is 7-segmented in the groundpattern of the family; ornamentation 0/4/5/2+Ae/1/1/9+Ae.

4.1.5. Leg 1

None of the species described above has an inner seta on the basis of leg 1. Meanwhile it was reported for some species and was observed by the authors on the type material of *Remaneicaris ignotus*. This should be seen, together with the presence of a row of spinules on the inner margin of leg 1 enp 1 (arrowed in Fig 3), as a plesiomorphic condition and composes the groundpattern of Parastenocarididae.

4.1.6. Male leg 3

A striking character observed for the three species described here is the presence of a 1-segmented enp on the inner margin of leg 3 basis in the male. Within *Remaneicaris* only *R. rhizophora* (Noodt, 1965) seems to lack the whole enp. Other species show a reduction of the enp. For example, *R. oncophora*, *R. analuizae* and *R. euniceae* display only 1 seta (no segment) at this position, a condition present in most parastenocaridids. Loss of the entire segment and even the seta is not unusual within the family. The presence of an enp segment, should be interpreted as a plesiomorphic character within Parastenocarididae. This, among other plesiomorphies, would suggest a basal position of the genus within the family, if we consider that all other Parastenocarididae share, as a synapomorphy, the loss of the enp in the male leg 3 and the setation of Mx2.

4.1.7. Male leg 4

Remaneicaris tridactyla n. sp., *R. paratridactyla* n. sp. and *R. juliae* n. sp. share with other members of *Remaneicaris* (viz. *R. remanei*, *R. hecate*, *R. sanctiludovicii* (Noodt, 1965), *R. icoaraci* (Noodt, 1963), *R. persephone*, *R. pluto*, *R. oncophora*, *R. rhizophora*, *R. paraguayensis*, *R. sierrae*, *R. cordobaensis*, *R. euniceae*, *R. analuizae*, *R. tageae* (Noodt, 1972) and *R. divae* (Noodt, 1972)), the similar leaf-shaped appearance of the leg 4 enp. With the exception of *R. euniceae*, *R. analuizae*, *R.*

tageae and *R. divae*, the species mentioned above have a row of spinules near the insertion of the male leg 4 enp (PERS) and a row of spinules on the inner margin of the male leg 4 basis (IBRS) (both arrowed in Fig. 4). These two characters can also be observed in *R. membranacea* (Noodt, 1965) and perhaps in *R. paraensis*. *Remaneicaris cordobaensis* and *R. ciliata*, as *R. membranacea* and *R. paraensis*, do not have the “typical” leaf-shaped leg 4 enp and can be characterized by the loss of the PERS. However, we believe that they belong to a large monophyletic group around *R. remanei*, all of them sharing the transformation of a seta on the male A1. The sexual dimorphism of the leg 4 enp is a synapomorphy of the family (Martínez Arbizu and Moura 1994), but it is difficult to reconstruct the condition in the groundpattern because of the extreme plasticity of this enp in regard to shape and size. In the groundpattern a terminal seta is still present on the leg 4 enp in the male.

4.1.8. Leg 5

Leg 5 of *R. tridactyla* n. sp., *R. paratridactyla* n. sp. and *R. juliae* n. sp. consists of a triangular plate in both sexes, with all the armature elements located on the outer side, due to the presence of a well-developed inner process on each limb. In *R. ignotus*, there is no inner cuticular process and the three elements are located in a distal position, conferring a square configuration on this limb. An incipient inner cuticular process on leg 5 is observed in *R. argentina*, *R. jujuyensis*, *R. drepanephora*, *R. palaciosi*, *R. clandestina* and probably *R. hurdi* (Jakobi and Silva, 1962). We believe that the evolutionary steps involved here are: Absence of an inner process, passing through an incipient inner process and finishing in a well-developed inner process on the leg 5. The absence of the intercoxal sclerite on leg 5 is a character present in the groundpattern of *Remaneicaris* and probably constitutes a synapomorphy for the genus. Associated with the lack of the intercoxal sclerite, there normally occurs a migration of both appendices to a ventro-lateral position. In *R.*

ignotus both legs 5 are located more ventrally, a character that we consider plesiomorphic within the genus. No sexual dimorphism should be expected in the groundpattern of *Remaneicaris*. Until now we can only say that the groundpattern for the family probably is composed by the leg 5 plates joined by a small intercoxal sclerite, as in *P. hispanica*, and without any sexual dimorphism.

4.1.9. Leg 6

In some members of *Remaneicaris* (viz. *R. sanctiludovici*, *R. sierrae*, *R. cordobaensis*, *R. ciliata*, *R. hecate*, *R. pluto*, *R. persephone*, *R. oncophora*), the leg 6 is a small flap armed with 2 setae covering the gonopore. As mentioned before, the presence of armature elements on P6 cannot be considered a plesiomorphy for Parastenocarididae, but as a synapomorphy for a group within *Remaneicaris*. Therefore, it does not compose the groundpattern for the family or even for the genus *Remaneicaris*.

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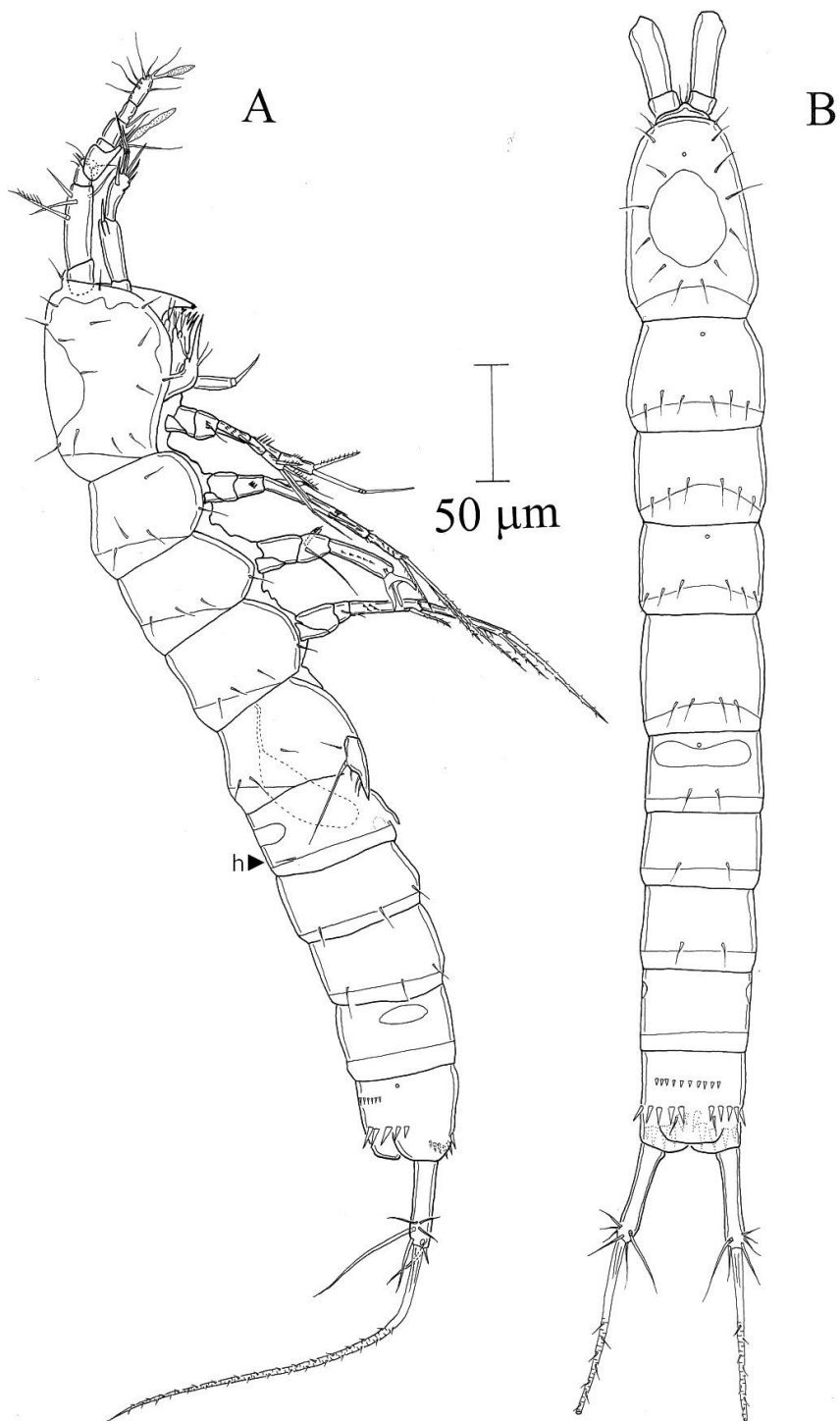


Figure 1- *Remaneicaris tridactyla* n. sp., male. A, habitus, lateral view; B, habitus, dorsal view. h= dorsal sensilla on the second male's urosomite.

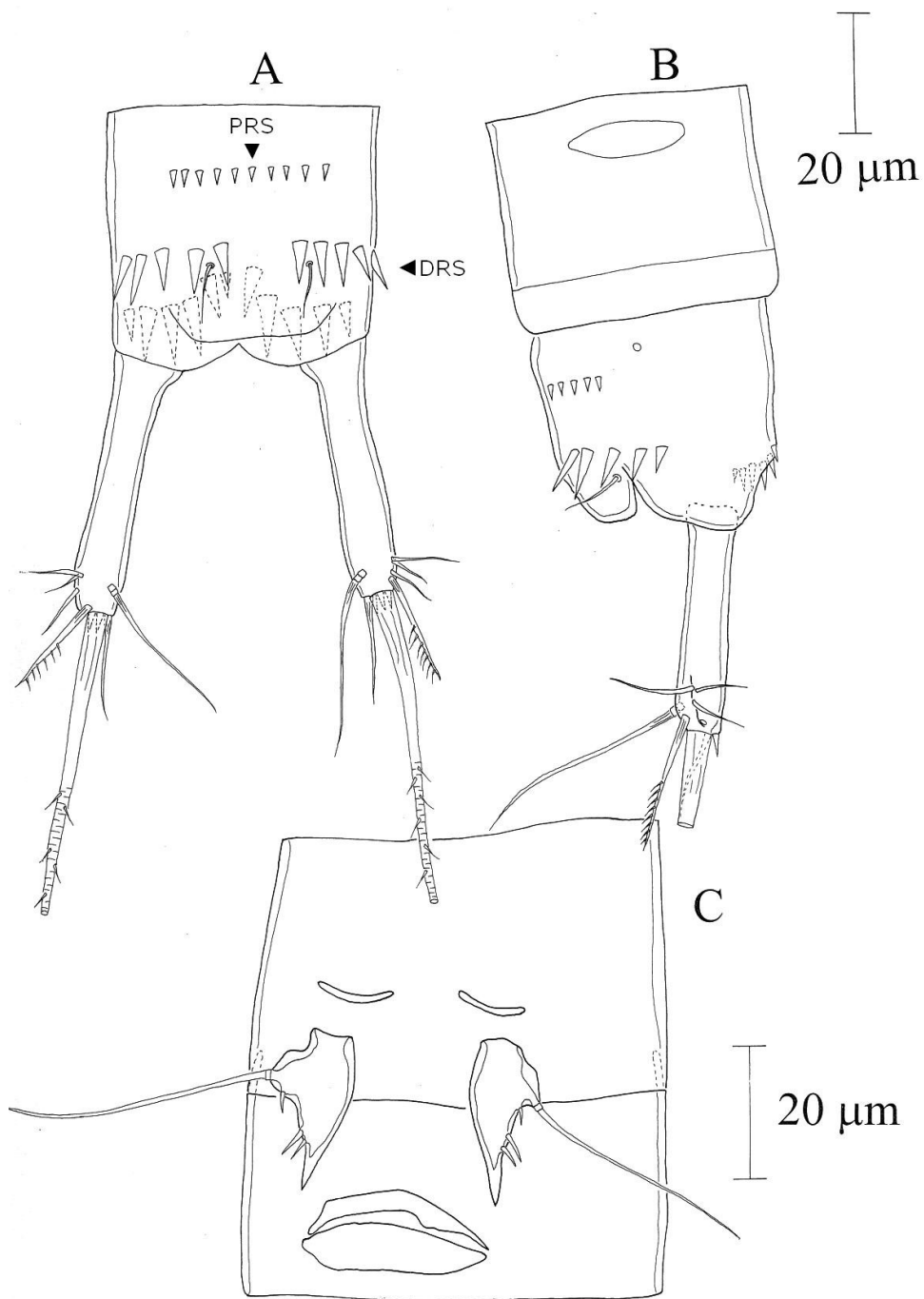


Figure 2- *Remaneicaris tridactyla* n. sp., male. A, telson, dorsal view; B, telson, lateral view; C, first urosomite with P5, ventral view. PRS= proximal row of spinules; DRS= distal row of spinules.

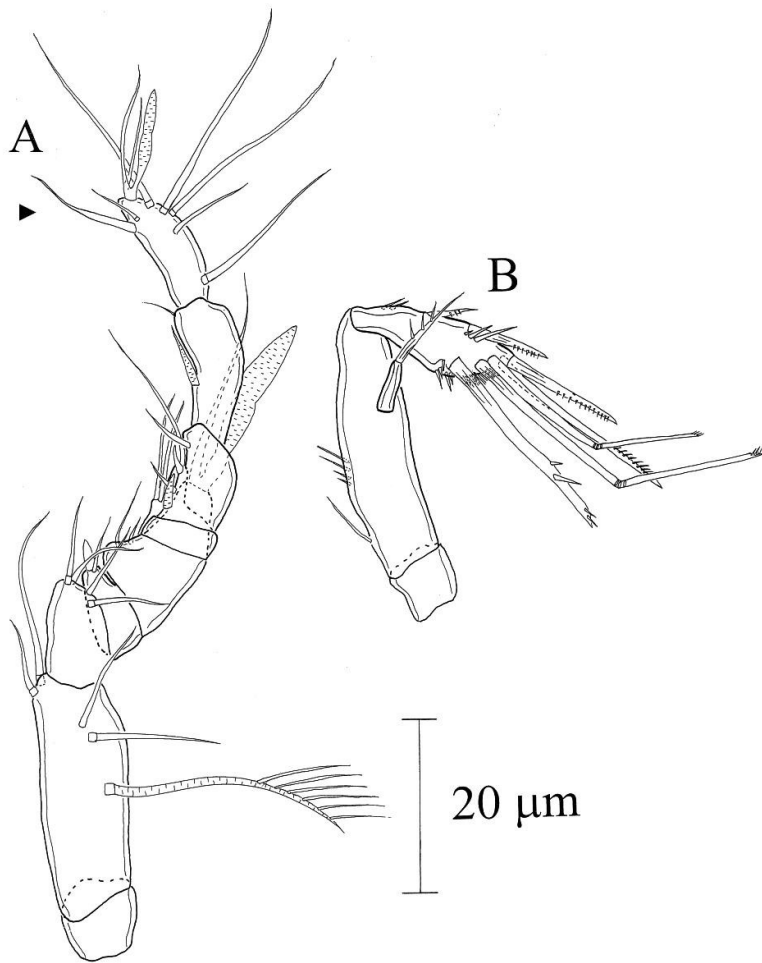


Figure 3- *Remaneicaris tridactyla* n. sp., male. A, antennule; B, antenna. Arrow indicating a modified seta on the last antennular segment.

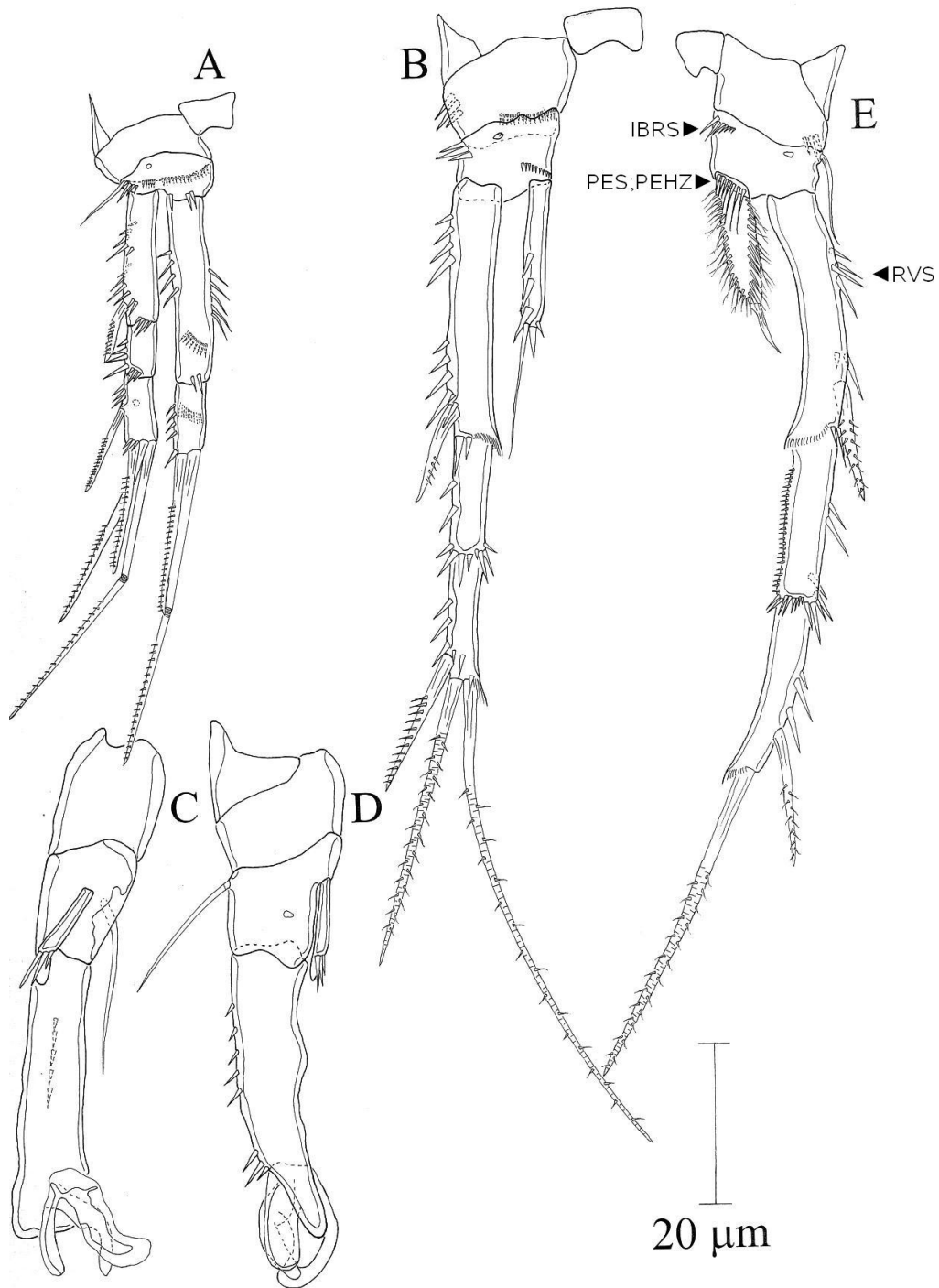


Figure 4- *Remaneicaris tridactyla* n. sp., male. A, leg 1; B, leg 2; C, leg 3, lateral; D, leg 3, frontal; E, leg 4. PES= pre endopodal spinules; PEHZ= pre endopodal hyaline zone; IBRS= inner basal row of spinules; RVS= row of "V" spinules.

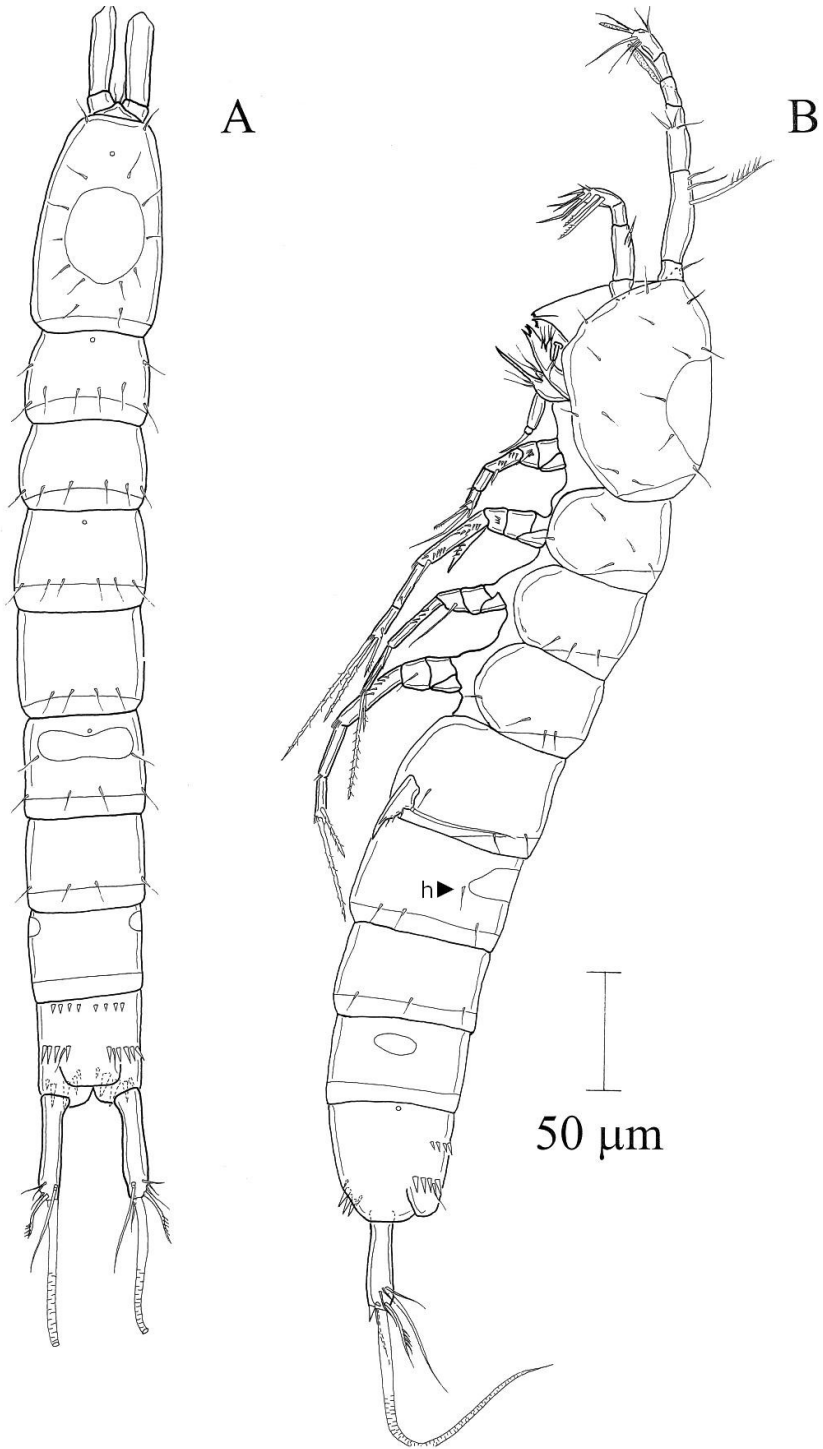


Figure 5- *Remaneicaris tridactyla* n. sp., female. A, habitus lateral; B, habitus dorsal.

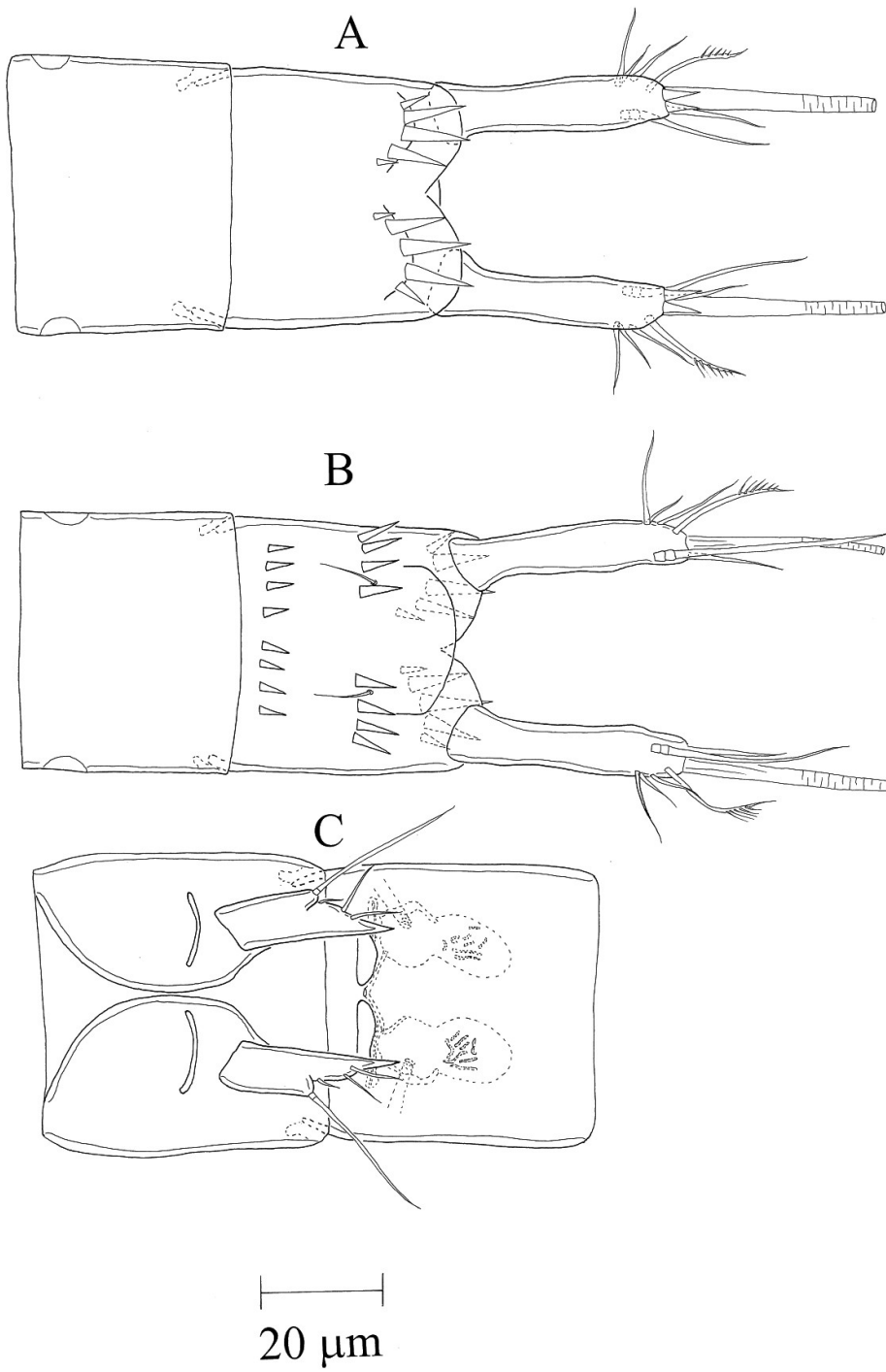


Figure 6- *Remaneicaris tridactyla* n. sp., female. A, telson, ventral view; B, telson, dorsal view, ; C, first urosomite with P5 and genital field, ventral view.

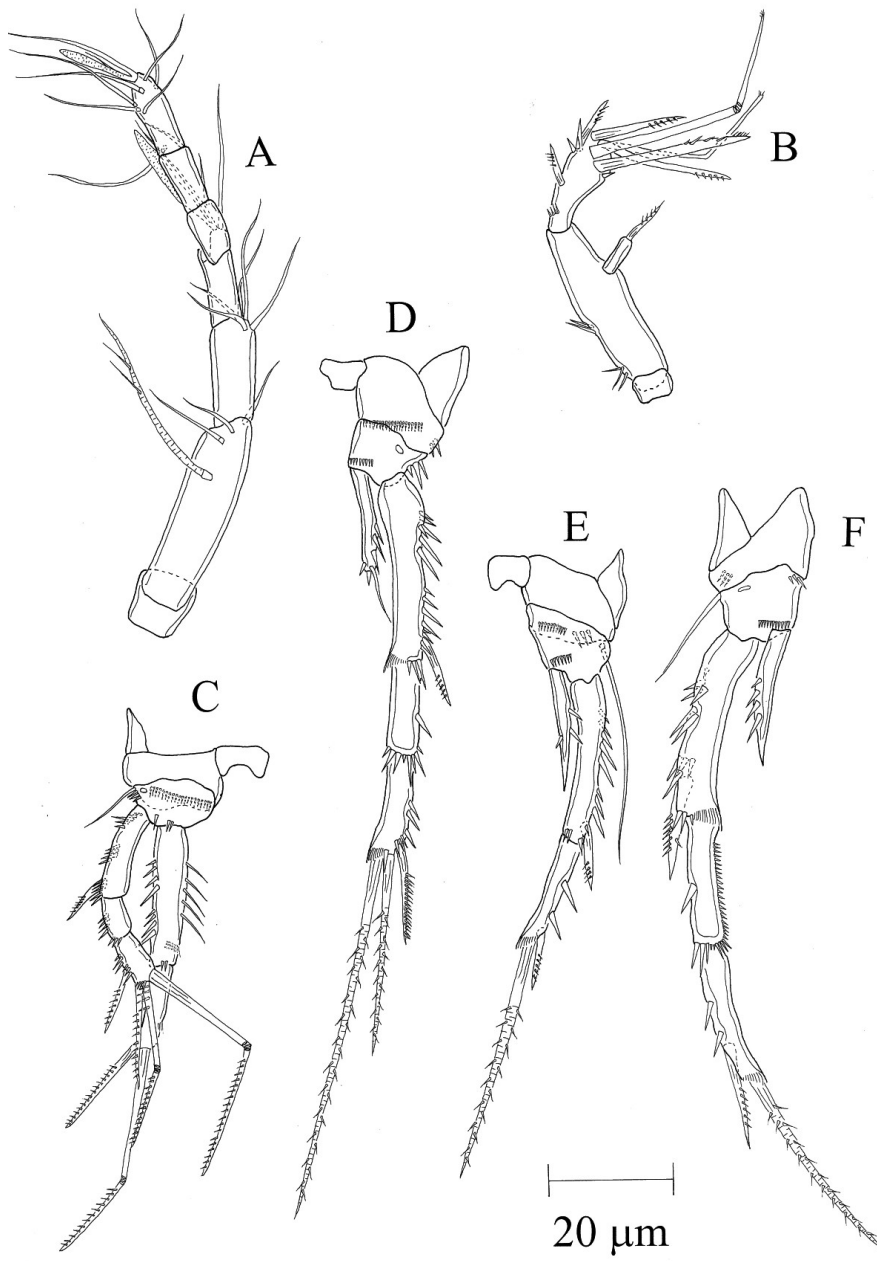


Figure 7- *Remaneicaris tridactyla* n. sp., female. A, antennule; B, antenna; C, leg 1; D, leg 2; E, leg 3; F, leg 4.

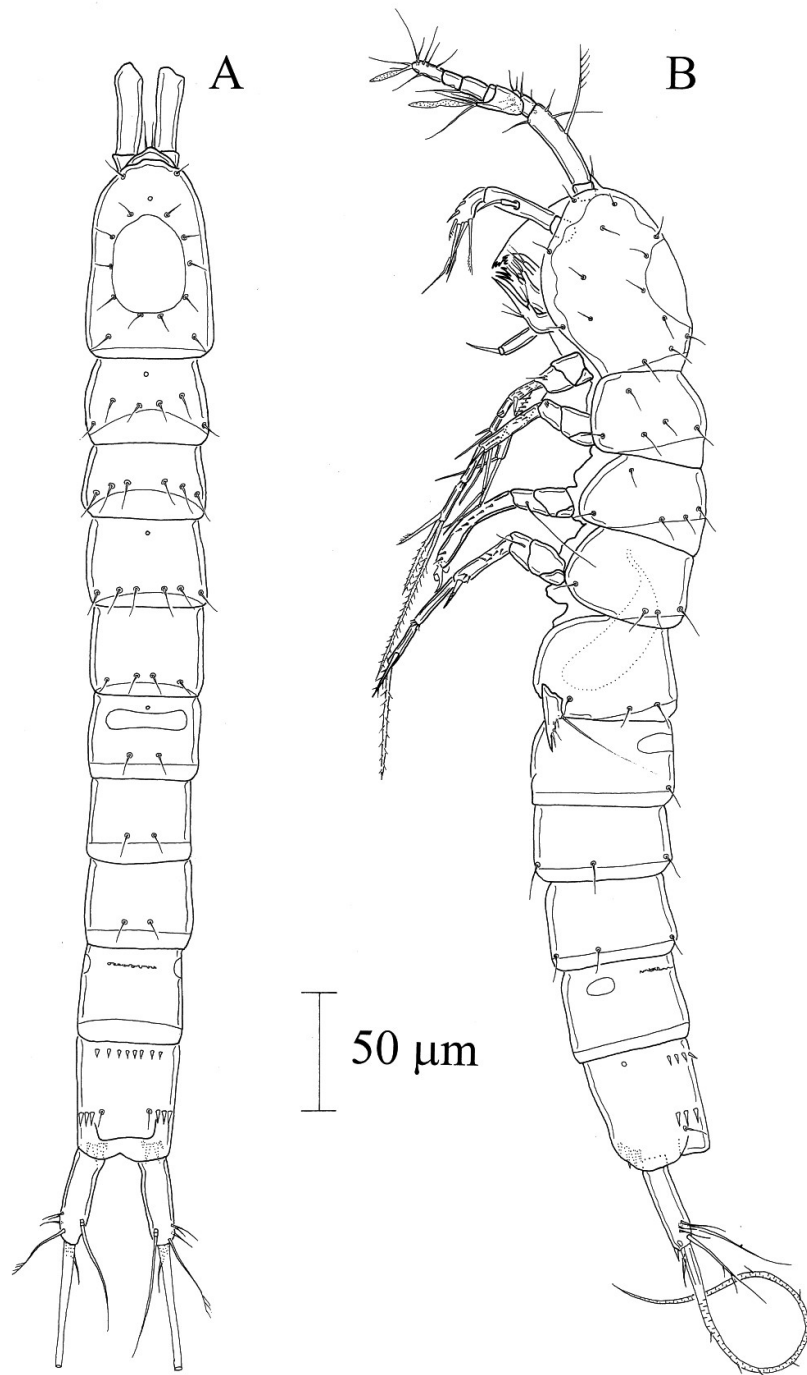


Figure 8- *Remaneicaris paratrindactyla* n. sp., male. A, habitus lateral; B, habitus dorsal.

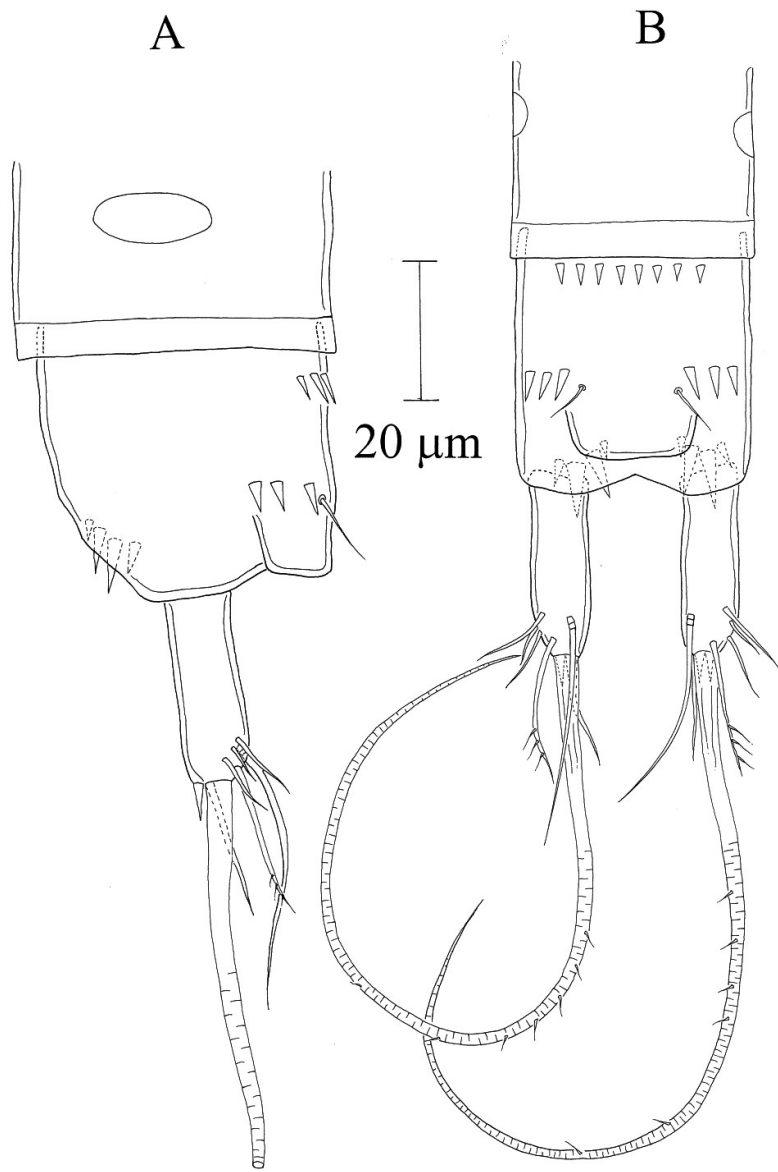


Figure 9- *Remaneicaris paratridactyla* n. sp., male. A, telson, lateral view; B, telson, dorsal view.

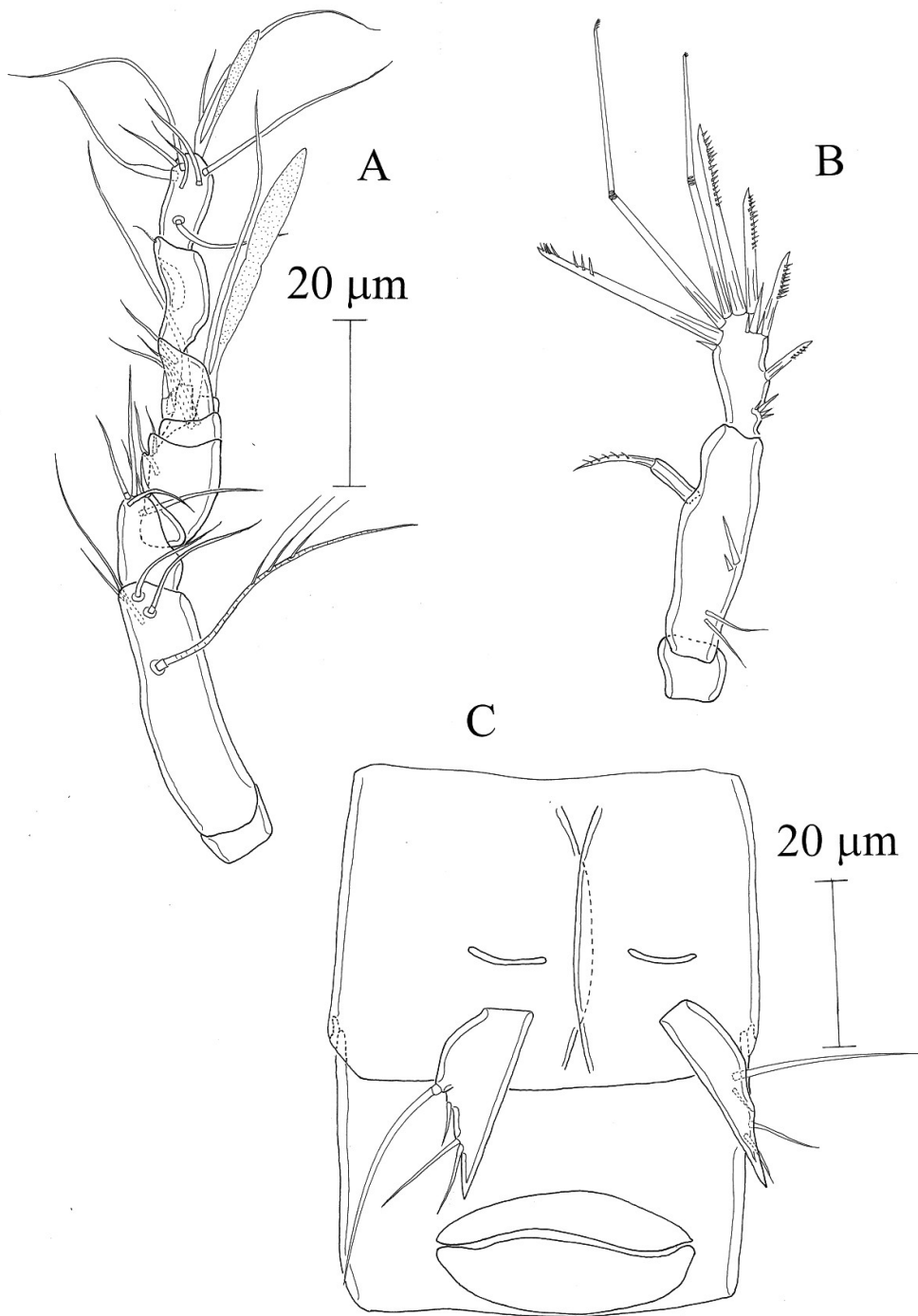


Figure 10- *Remaneicaris paratridactyla* n. sp., male. A, antennule; B, antenna; C, ventral view of first urosomite with P5.

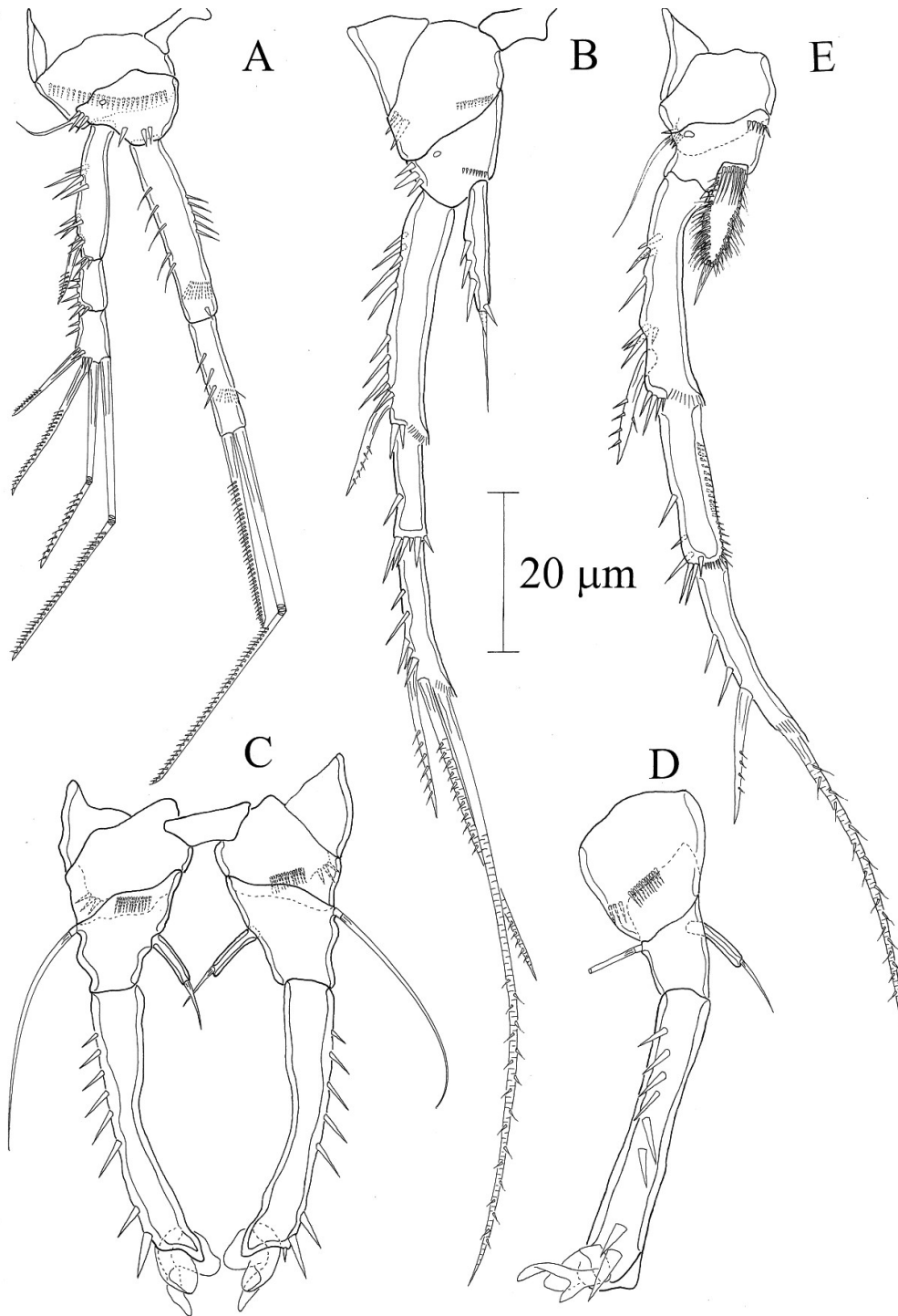


Figure 11- *Remaneicaris paratridactyla* n. sp., male. A, leg 1; B, leg 2; C and D, leg 3; E, leg 4.

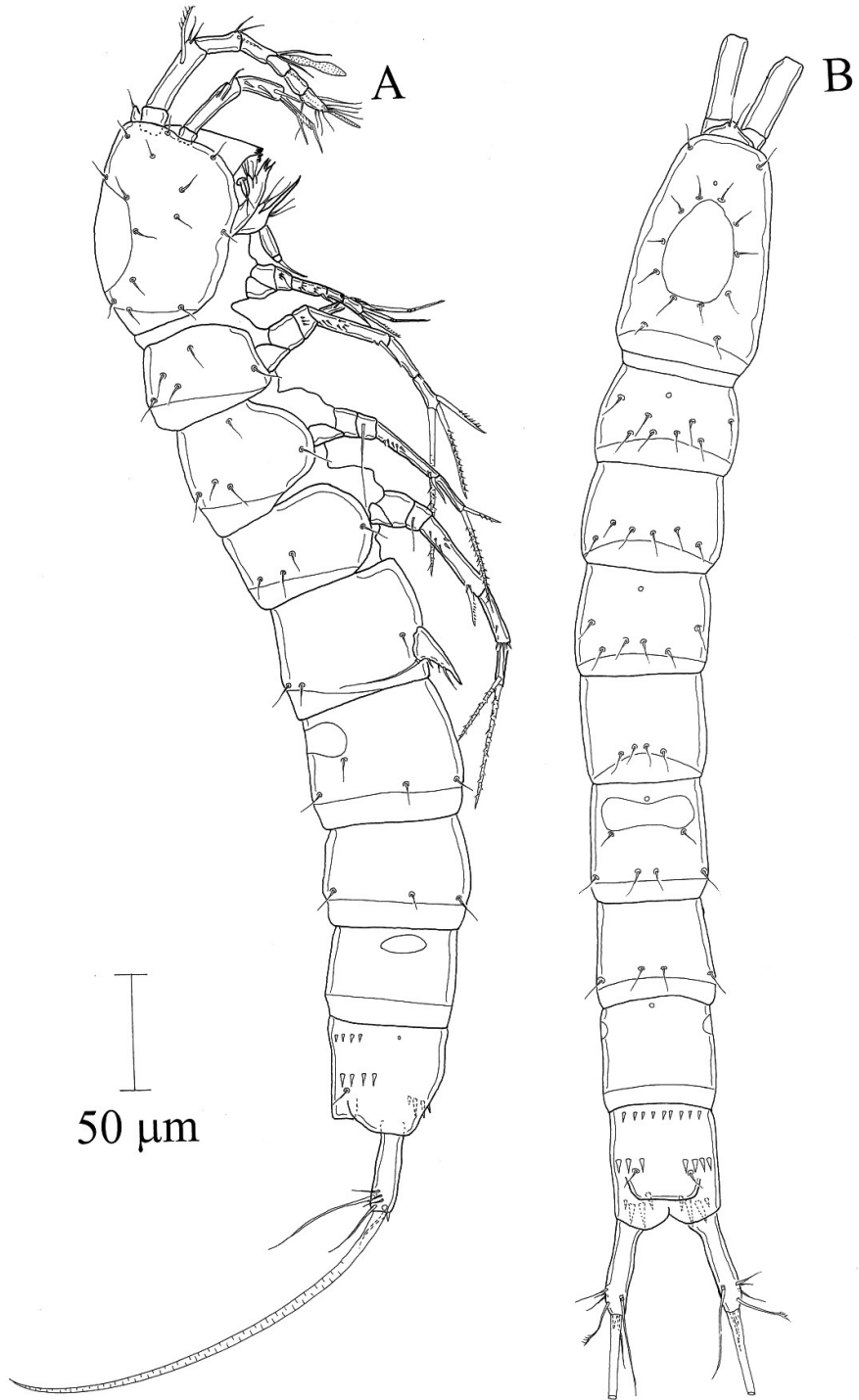


Figure 12- *Remaneicaris paratridactyla* n. sp., female. A, habitus lateral; B, habitus dorsal.

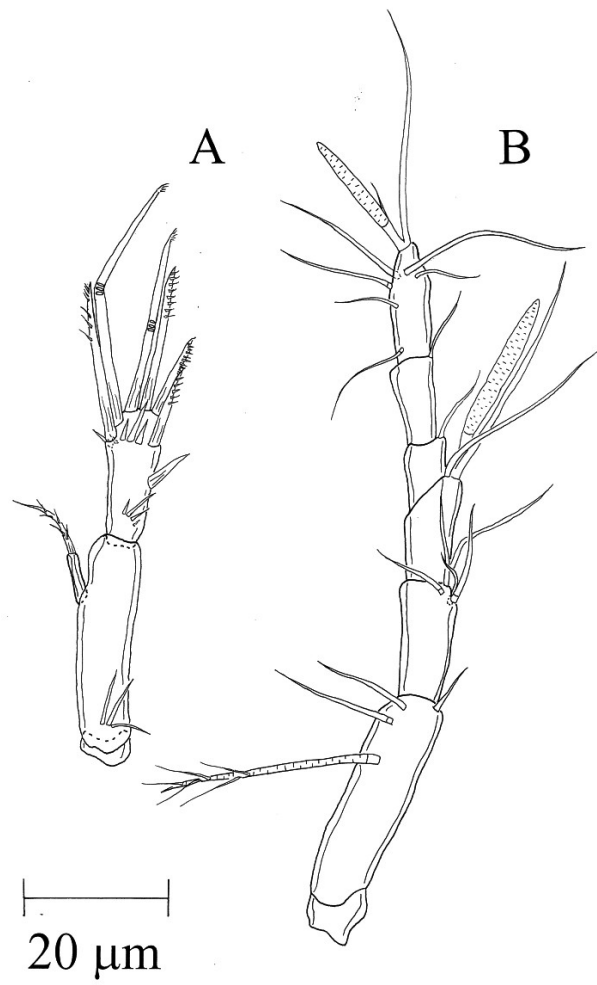


Figure 13- *Remaneicaris paratridactyla* n. sp., female. A, antenna; B, antennule.

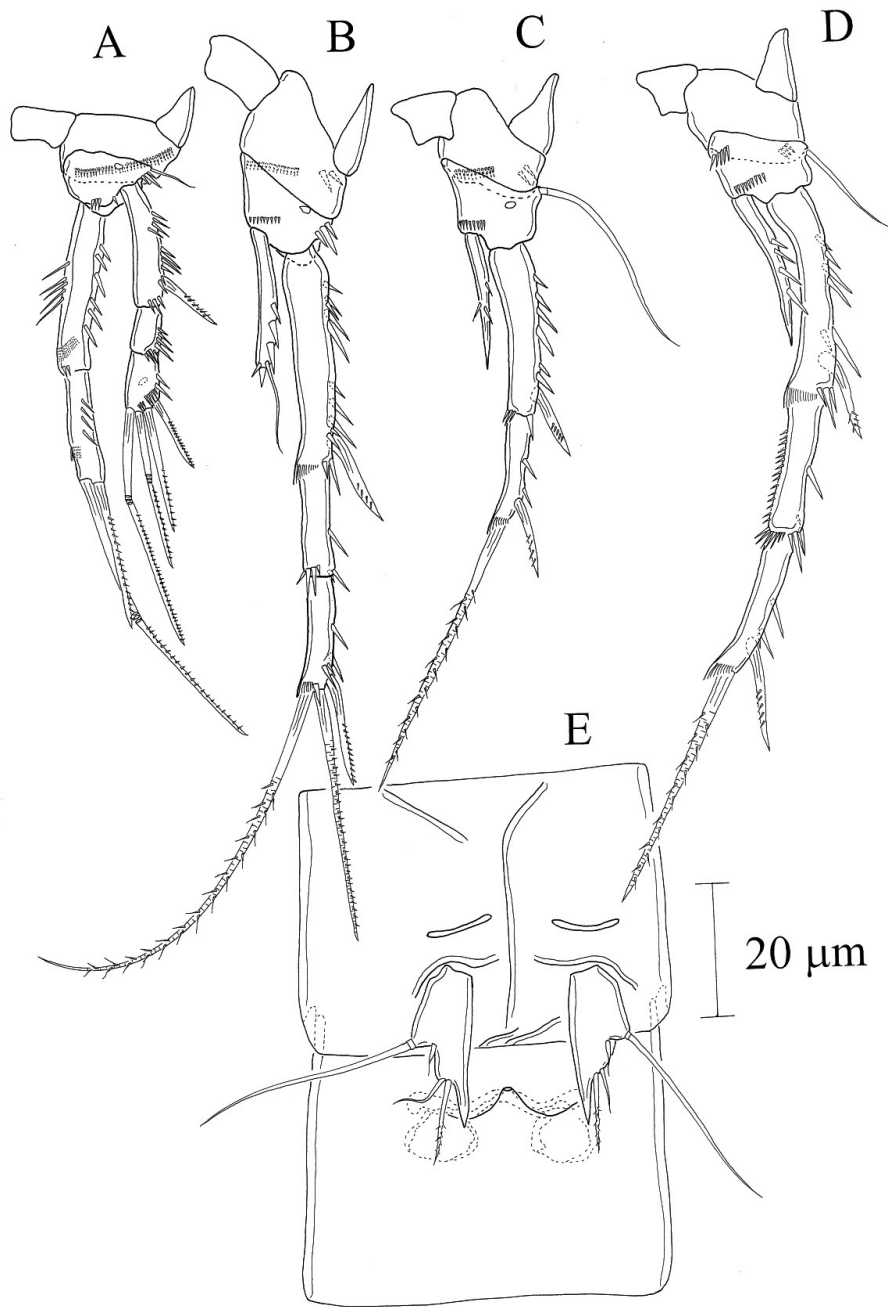


Figure 14- *Remaneicaris paratridactyla* n. sp., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5.

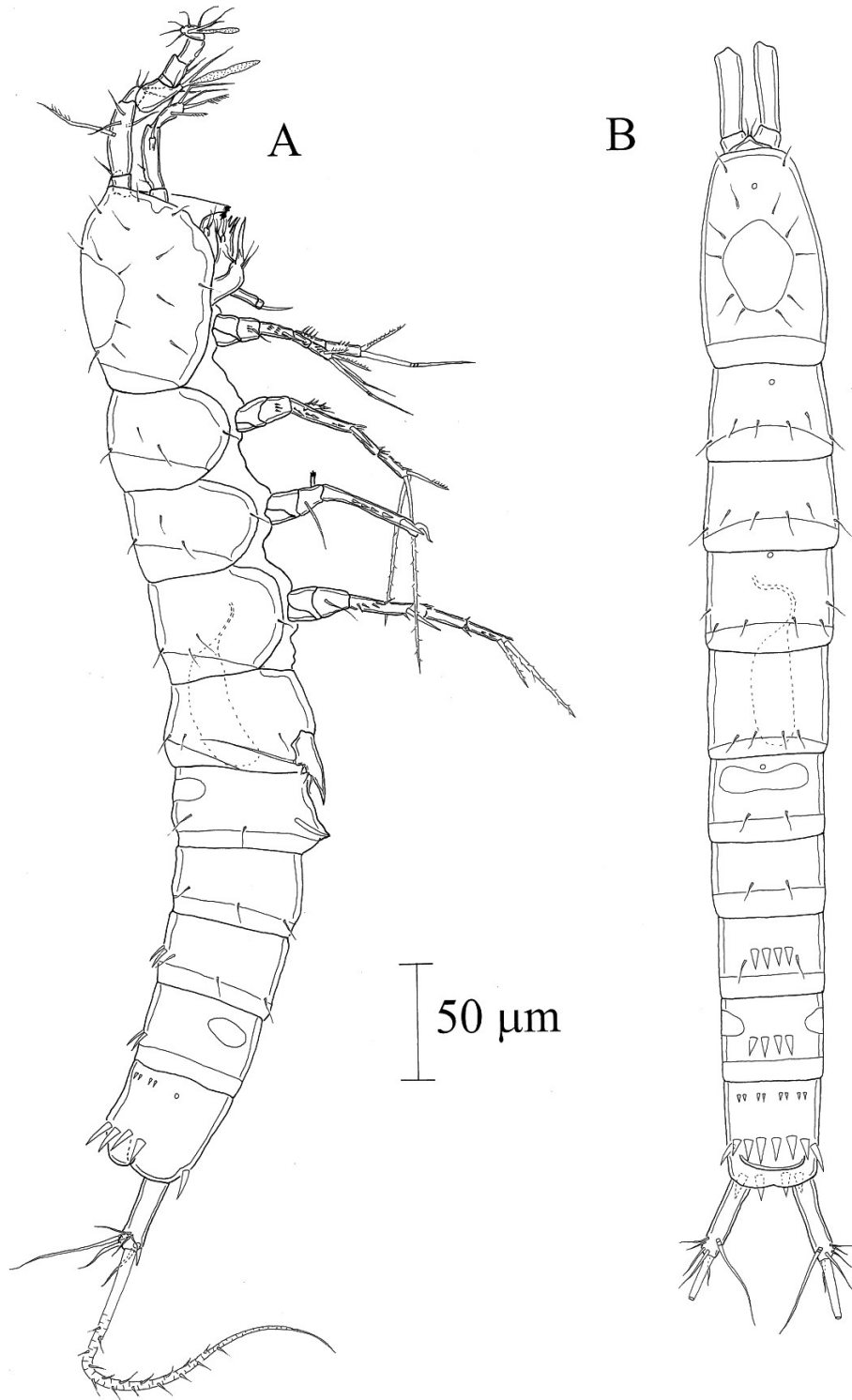


Figure 15- *Remaneicaris juliae* n. sp., male. A, habitus lateral; B, habitus dorsal.

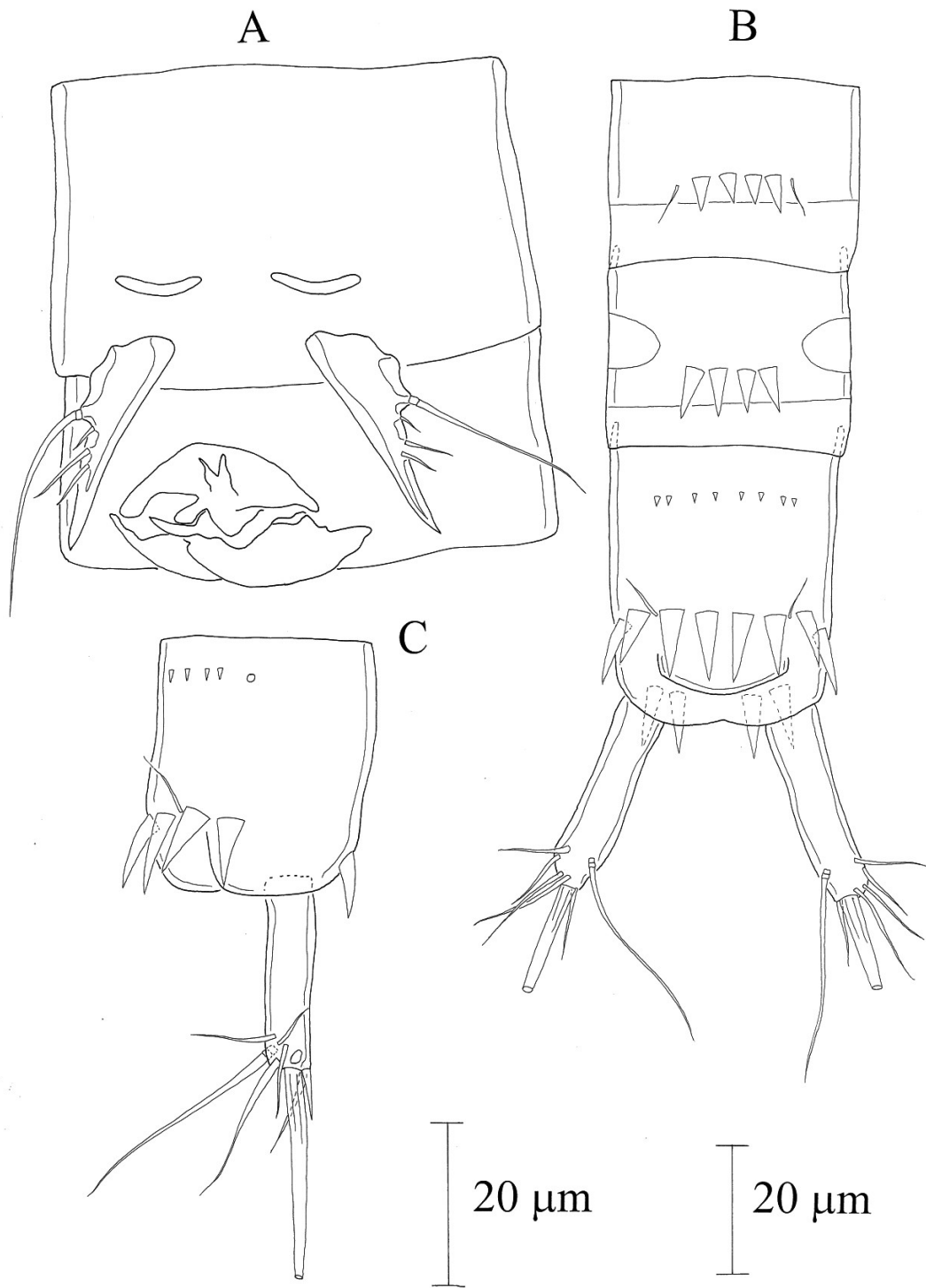


Figure 16- *Remaneicaris juliae* n. sp., male. A, ventral view of first urosomite with P5; B, telson, dorsal view; C, telson and previous urosomites, lateral view.

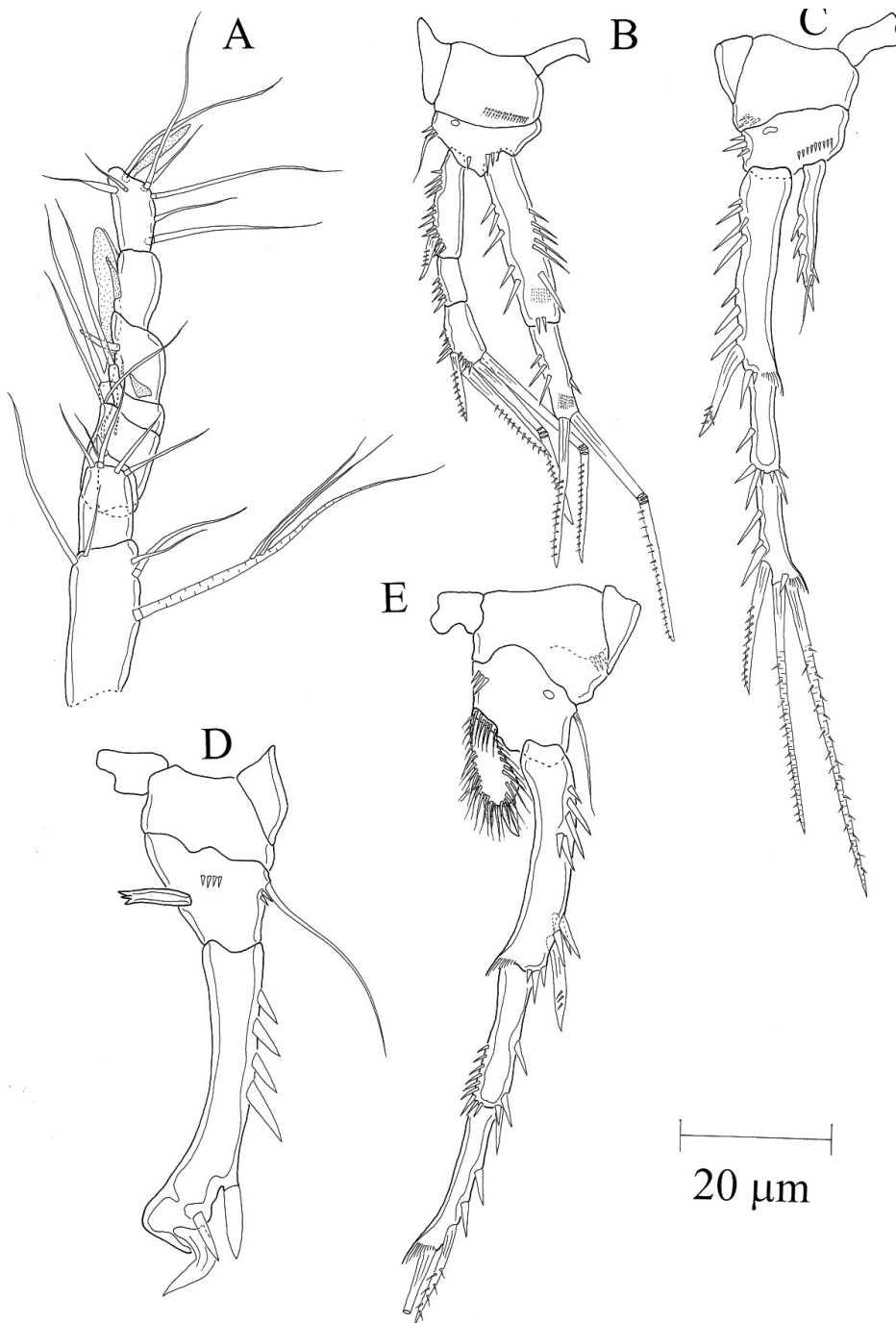


Figure 17- *Remaneicaris juliae* n. sp., male. A, antennule; B, leg 1; C, leg 2; D, leg 3; E, leg 4.

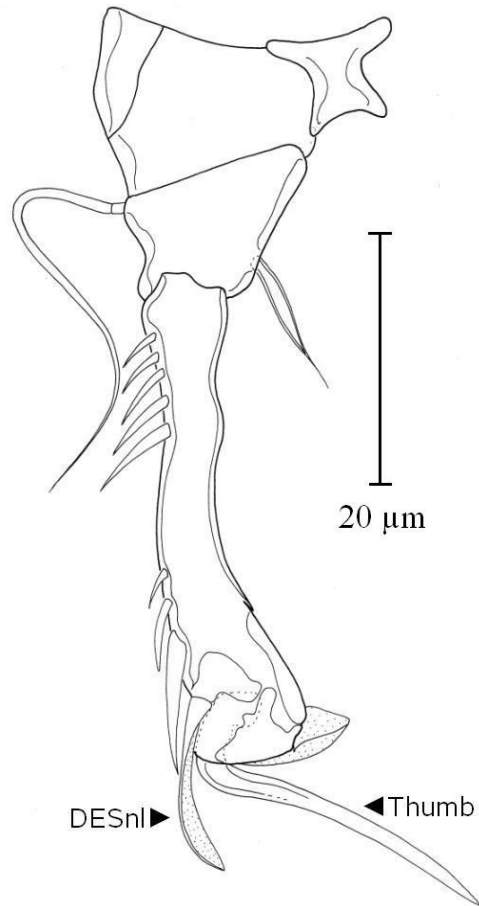


Figure 18- *Remaneicaris argentina* (Noodt, 1965), male, leg 3. DESnl= distal exopodal spinule.

Chapter III

Redescription of *Remaneicaris ignotus* (Dussart, 1983), a Parastenocarididae (Copepoda, Harpacticoida) with an unusual set of plesiomorphic characters

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Abstract:

In the course of a phylogenetical analysis of the family Parastenocarididae we re-describe here both sexes of *Remaneicaris ignotus* (Dussart, 1983) and its phylogenetic position within the genus *Remaneicaris* is briefly discussed. This species can be distinguished from the other species of the genus by the following autapomorphies: absence of an outer seta on the basis of the leg 1 in both sexes; presence of a very chitinized and perforated cuticle; presence of a less chitinized plate between the fifth leg, not homologous to the intercoxal plate and the presence of an irregular shaped leg 4 enp on males, hirsute on the proximal outer margin and with a distal hyaline seta. It can be easily identified as well by the presence of some unusual plesiomorphic characters, unknown so far from any other member of the genus. In this sense, we can mention the presence of a dorsal integumental window on all urosomites, an inner seta on the basis of leg 1 in males and females, the

ventral position of leg 5 and the linear distribution of the proximal outer row of spinules on exopodite 1 of legs 2 and 4.

Keywords: *Remaneicaris ignotus*, Parastenocarididae, South America, Groundwater, plesiomorphies

Introduction:

The genus *Remaneicaris* Jakobi, 1972 is, until now, the most diverse group of Parastenocarididae in Latin America, with 31 already described species. The geographical distribution of its composing species extends from Argentina (Patagonia) to El Salvador (Central America), being *R. psammae* (Rouch, 1962) the most meridional species, while *R. meyerabichi* (Noodt, 1962) and *R. palaciosi* (Noodt, 1962) show the most northern distribution.

Members of *Remaneicaris* share, as synapomorphy, some peculiar characters such as the subdistal position of the outer spine on the exopodite 3 of leg 4, the absence of an intercoxal sclerite on leg 5 and a mesially located spinule on the third exopodite of leg 2 and 4. Additionally, most of them have also the presence of a lateral integumental window on each side of the last urosomite (Corgosinho and Martínez Arbizu 2005). They also share an unusual set of plesiomorphic characters within the family such as a nine-segmented antennule in males, first endite of maxilla with two setae, second endite with three slender setae and leg 3 of males with one-segmented endopod.

Groundwater copepods from Argentina were primarily studied by Noodt (1965) and later by Dussart (1983). This fauna resulted to be very diverse, being represented by species from different evolutionary lineages within *Remaneicaris*. Most of the species described by Noodt, with the only exception of *R. argentina* (Noodt, 1965) and *R. jujuyensis* (Noodt, 1965) belong to a more derived group within this genus. However, in samples taken from Laguna Sirena (province of Corrientes),

Dussart (1983) found a very peculiar parastenocaridid and described it as *Parastenocaris ignotus* Dussart, 1983; later it was transferred to the genus *Remaneicaris* by Corgosinho and Martínez Arbizu (2005). Within this genus, *R. ignotus* shows a special set of plesiomorphic characters not known so far from any other member and which indicate its basal position within the genus.

In this work we redescribe both sexes of *R. ignotus* and the presence of some unusual plesiomorphic characters within the genus is discussed.

Material and methods:

Type species of *R. ignotus* was loaned from the collection of the Museum National d'Histoire Naturelle (Paris). Due to the bad state of the type species, the redescription was based on the observation of paratypes dissected by the authors. Animals were dissected in lactic acid and mounted on slides in glycerine. Drawings were made with a Leica DMR microscope, with Normarsky interference contrast and using a drawing tube, at 400x and 1000x magnification.

Abbreviations: A1 = antennule, A2 = antenna, Ae = aesthetasc, Md= mandible, Mx1= Maxillule, Mx2= Maxilla, Mxp= maxilliped, endopod= enp, exopod= exp, synR= synapomorphy of *Remaneicaris*, aut= autapomorphy.

Systematics

Family Parastenocarididae Chappuis, 1940

Genus *Remaneicaris* Jakobi, 1972

***Remaneicaris ignotus*.**

Synonym and references: *Parastenocaris ignotus* Dussart, B. H. (1983) *Comunicaciones Cientificas CECOAL*, 16, 1-8.

Parastenocaris ignotus Corrales de Jacobo, M. A. and Frutos, S. M. (1985) *Physis*, 104, 43-48.

Remaneicaris ignotus Corgosinho, P. H. C. and Martínez Arbizu, P. (2005) *Senckenbergiana Biologica*, 85(2), 147-162.

Material: Holotype- 1 partially dissected male, mounted in two slides and deposited at Muséum national d'Histoire naturelle (MNHM; Paris, France), labelled MNHM-CP666. Paratypes- One male dissected and mounted on seven slides, labelled MNHM-CP2204; one female dissected and mounted on 7 slides, labelled MNHM-CP2205; one undissected female mounted on 1 slide MNHM-CP2206; one undissected female mounted on 1 slide MNHM-CP2207 and 7 females from the same locality as the holotype, preserved in alcohol and deposited at MNHN (Paris, France), under the number MNHM-CP928.

Distribution: Laguna Sirena, among the cities of Itá Ibaté and Ituzaingó (Corrientes province, Argentina).

Diagnosis: Parastenocarididae with 9-segmented antennule in males and 7-segmented in females. Dorsal integumental windows on cephalothorax, 2nd-5th urosomite of males and 2nd-4th of females. Cuticle thick and perforated. Telson not ornamented. Mx2 with two setae on the first endite and three slender setae on the second. Leg 1 without sexual dimorphism and with a seta on the inner margin of basis. Exp 1 of legs 2 and 4 with a linear row of spinules, proximally, on the outer margin. Third exp of legs 2 and 4 with a spinule mesially placed on the outer margin. Leg 3 with 1-segmented enp; exp slightly curved, without ornamentation on the outer margin; apophysis short and rounded; thumb strong and s-shaped. Leg 4 with a subdistal seta on the outer margin of exp 3; enp of males with an irregular shape, proximally hirsute and with a distal hyaline seta. Leg 5 small, quadratic, ventrally positioned, with all setae distally located and without an intercoxal sclerite.

Description: Male. Habitus (Fig. 1 A, B). Length 410 μ m (measured from the tip of rostrum to the distal rim of anal operculum). Body heavily chitinized and with cuticular perforations along the entire surface. Rostrum not fused to cephalothorax, with a wide base and two sensilla on the tip. Cephalothorax and urosomites with 1 dorsal integumental window each. Dorsal pores on cephalothorax, thoracic somites 1 and 3 and second urosomite. One pair of lateral pores on telson. For sensilla on tergites see fig. 1 A and B. Telson longer than wide (Fig. 1 A, B and Fig. 2 A, B), approximately as long as two previous somites together. Anal operculum smooth and slightly concave (Fig. 1B and 2B). Furca (Fig. 1A, B and Fig. 2 A, B) about 4 times as long as wide, with 7 setae, all of them located on the distal third. A1 (Fig. 3 A) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/1/5+Ae/1/3/1?/9+Ae; one hyaline spine on the 7th and 8th segments. A2 (Fig. 3 D) with allobasis; exp 1-segmented with 1 seta, and 1-segmented enp bearing an anterior hyaline frill and 7 setae. Bucal parts ornamentation as follows (Fig. 3E): Md with a coxal gnathobasis bearing 1 seta and a palp with 2 setae; Mx1 with a precoxal arthrite with 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines and 1 slender seta), coxa with 1 seta and basis with 3 setae; Mx2 with two setae on the proximal endite and three slender setae on the distal endite, enp with two setae, one is broken on the right limb; Mxp 3-segmented, distal segment with 1 claw-like seta. Leg 1 (Fig. 4 A) coxa unarmed, with 2 rows of spinules on the posterior side; basis without outer seta, with an anterior pore, 3 spinules on the outer margin, 4 distal spinules anterior to the insertion of the enp and an inner seta; enp 2-segmented, first segment without ornamentation on the inner margin, with 2 rows of 2 spinules on the outer margin and a posterior hyaline frill; segment 2 with a posterior hyaline frill and 2 distal setae, one of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Coxa of Leg 2 (Fig. 4 B) unarmed, with 2 rows of spinules on the posterior side; basis without outer seta, ornamented with 1 row of spinules on the outer margin, 1 row of spinules near the insertion of

the enp and 1 anterior pore near the outer margin; exp 3-segmented; segment 1 with an outer spine, a hyaline frill on the inner margin and with a linear row of spinules, proximally, on the outer margin (arrowed), segment 2 without armature, segment 3 broken (originally like in the female, with 3 setae, a distal hyaline frill on the inner corner and two spinules located mesially on the outer margin); enp 1-segmented with 1 subdistal seta and 3 distal spinules. Leg 3 (Fig. 4C) coxa unarmed and without ornamentation; basis with an outer seta and an anterior row of big spinules running diagonally; enp unisegmented with one fused seta; exp 1-segmented, elongate, without spinules along the outer margin, with 1 subdistal strong and curved seta (thumb); apophysis rounded. Leg 4 (Fig. 4 D) coxa unarmed, basis with an outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 with an outer spine inserted distally and with the proximal row of spinules linearly arranged (arrowed) on the outer margin, segment 2 without armature, segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and two spinules located mesially on the outer margin; enp 1-segmented, irregular, hirsute, with two inner protuberances and a distal hyaline seta. Leg 5 (Fig. 4E) quadratic and without an inner spinulose process, ventrally located, and without an intercoxal sclerite. A less cuticularized zone, without any articulation with the leg 5, can be observed between the two limbs (Fig. 4 E, arrowed).

Female: Sexually dimorphic in A1, leg 3, leg 4, leg 5 and genital field.

Female. Habitus (Fig. 5 A). Length 424 μ m (measured from the tip of rostrum to distal rim of the anal operculum). Rostrum as in male. Cephalothorax, double genital somite and subsequent urosomites with 1 dorsal integumental window each. Dorsal pores as in males and one pair of lateral pores on the telson. For sensilla on tergites see fig. 5 A. Telson, furca (Fig. 5 A) and body chitinization as in male. A1 (Fig. 6 E) 7-segmented; number of setae beginning at the proximal segment: 0/5/4/2+Ae/1/0?, probably 1/9+Ae. A2 like in male, with allobasis; 1-segmented exp with

1 seta, 1-segmented enp bearing 7 setae and a posterior hyaline frill. Leg 1 and leg 2 (Fig. 6 A and B) as in male. Leg 3 (Fig. 6 C) coxa unarmed, with a row of posterior spinules; basis with an outer seta, an anterior pore, a row of spinules near the insertion of the enp and one row between the exp and the outer seta; exp 2-segmented, segment 1 with an outer spine, segment 2 with 1 spine and 1 seta; enp 1-segmented and spiniform. Leg 4 (Fig. 6 D) exp as in male; basis with a row of small spinules near the insertion of the enp; enp spiniform with 1 incorporated distal seta. Leg 5 (Fig. 5 B) quadratic, with a small spiniform process on the inner side. Genital field as illustrated in Fig. 5 B, with a single mesially located copulatory pore. Gonopore is a transversal slit.

Discussion

Remaneicaris ignotus differs from the other species of the genus by the following synapomorphies: absence of an outer seta on the basis of the leg 1 in both sexes; presence of a very chitinized and perforated cuticle; presence of a less chitinized plate between the fifth legs, not homologous to the intercoxal sclerite and the presence of an irregular leg 4 enp on males, hirsute on the proximal outer margin and with a distal hyaline seta.

The absence of an outer seta on the basis of leg 1 is a very interesting character, rarely appearing within the family. Within *Remaneicaris*, only *R. ignotus* have such character and the presence of this seta on the outgroup of Parastenocarididae (viz. *Psammonitocrella* Rouch, 1992; see Martinez Arbizu and Moura 1994), as well as in most of the described species of this family, suggests that absence of an outer seta on the basis of leg 1 is a character that appeared independently within the family, not composing, therefore, its groundpattern.

According to Dussart (1983), this species should be considered closely related to *Parastenocaris sioli* Noodt 1963 (hereafter *Siolicaris sioli* (Noodt, 1963); see ICZN, article 13) due to some “similarities” found in the furca. However, according to the same author, “...considering the

endopodites, it would be better to group it with those species from the *remanei*-group...” (free translation). In our opinion, the morphology and ornamentation of the furca is not a phylogenetically informative character within the family, as already pointed out by Schminke (1991). This author demonstrated that the shape of the furca can be very variable, even between members of the same species, sometimes showing a very strong sexual dimorphism. In fact, in some descriptions of Noodt, such as the “aberrant” forms of *Brasilibathynellocaris panamericana truncata* (Noodt, 1962), *Brasilibathynellocaris salvadorensis lanceolata* (Noodt, 1962) as well as in some *Remaneicaris* species such as *R. paraensis bulbifera* (Noodt, 1963), *R. paraguayensis phylloides* (Noodt, 1963), *R. ciliata* (Noodt, 1965) and *R. sanctiludovicii* (Noodt, 1965), we can observe a strong sexual dimorphism, occurring, in the females, both the normal and the transformed furca, even in the same population. There are also few cases of transformed furca in males (Schminke 1991). In other species, outside the Neotropical Region, this phenomenon also occurs (viz. Schminke 1991). Besides, a closer observation of this structure reveals that in *R. ignotus*, as well as in all other *Remaneicaris* species, the dorsal seta (seta VII) occurs at the same level of the setae I, II and III, a character not found in *Siolicaris sioli*. In this species, as well as in some other related Neotropical genera, the dorsal setae occurs, normally, in a more distal position, while the setae I, II and III have a more proximal arrangement.

Also, members of *R. ignotus* differ from *Siolicaris* as well as from the other Parastenocarididae by the subdistal position of the outer seta of the 3rd exp of leg 4 (synR; for a discussion about convergent appearance of this character, see Corgosinho and Martinez Arbizu 2005), as well as by a set of other derived and plesiomorphic characters that were observed only in members of *Remaneicaris*. We can mention the presence of an endopod on the leg 3 of males (pl), the presence of at least one big spinule mesially placed on the outer margin of the third exopodite of the legs 2 and 4 (synR), leg 5 without intercoxal sclerite (synR) but with a less chitinized plate

between these limbs, and not connecting them (aut), first endite of Mx2 with two setae (pl) and the presence of three slender setae on the second endite of Mx2 (pl).

These characters associated to the Mx2 are particularly interesting to reconstruct the phylogeny of the family, since all other Parastenocarididae, including *S. sioli*, share, as a synapomorphy, the presence of only one seta on the first endite of Mx2, while in the second endite, one seta is transformed into a serrated spine. Another synapomorphy of the remaining Parastenocarididae is the absence of an enp on the leg 3 of males.

Although considered as a typical *Remaneicaris*, *R. ignotus* shows a set of unusual plesiomorphic characters within the genus and the lack of less inclusive synapomorphies with other groups of species within *Remaneicaris* let us assume that it should occupy the most basal position in the genus. Thus, in accordance with Corgosinho (2007) this species is the sister-taxon of a group including *R. meyerabichi* plus all other *Remaneicaris* species, viz. (*R. ignotus* (*R. meyerabichi* (*Remaneicaris* spp))).

In accordance with Corgosinho and Martínez Arbizu (2005), the presence of integumental windows seems to be a character present in the groundpattern of Parastenocarididae according to the following pattern: 1 dorsal window on the cephalothorax, 1 dorsal window on urosomites 2-5, in males, and urosomites 2-4, in females (due to the genital double somite). Within *Remaneicaris* almost all species show dorsal integumental windows on the cephalothorax, second urosomite and a single lateral integumental window on the fifth urosomite although in some undescribed species this window can split into two lateral windows on each side of the body. Other patterns can also be seen within the genus. For example, *R. analuizae* Corgosinho and Martínez Arbizu, 2005 shows, besides the common integumental lateral window of the fifth urosomite, a lateral window also on the previous urosomite and in *R. pluto* (Noodt, 1965), *R. hecate* (Noodt, 1965), *R. persephone* (Noodt, 1965) and *R. oncophora* (Noodt, 1965) the dorsal window of the second urosomite is divided into

two smaller windows located on the latero-dorsal margin of the somite. Within *Remaneicaris*, only *R. ignotus*, *R. meyerabichi* and *R. palaciosi* have dorsal window in more than one urosomite; although one dorsal window on each urosomite can be seen only, within *Remaneicaris*, in *R. ignotus*. In *R. meyerabichi* and *R. palaciosi*, considering only the males, a dorsal integumental window occurs only in the cephalotorax and urosomites 2 and 5.

As already mentioned by Corgosinho and Martínez Arbizu (2005), it seems that there are several steps involved in these transformations that could be of phylogenetic relevance. These authors mentioned the “elongation” of the dorsal urosomal windows to the lateral position, the splitting of the dorsal windows on urosomites 4 and 5 into lateral windows, the loss of the windows on the fourth urosomite, and the loss of the windows on the third urosomite. At this moment, however, new data based on a phylogenetic reconstruction of the genus (Corgosinho 2007) brought new light to this scenario. Thus, it is more parsimonious to assume that the steps involved are: first, the loss of the dorsal integumental windows on urosomites 3 and 4, keeping dorsal in the 5th urosomite. This condition is present in *R. meyerabichi* and composes the groundpattern of the clado (*R. meyerabichi* (*Remaneicaris* spp)). The second step involves the splitting of the dorsal integumental window of the 5th urosomite into lateral windows, being it in the groundpattern of a clado formed by (*Remaneicaris* spp). The third and last step occurs in a more derived group within the clado (*Remaneicaris* spp) and is represented by the splitting of the dorsal integumental window of the 2nd urosomite into two dorsolateral windows. Other observed patterns, such as the presence in *R. analuizae* of a lateral integumental window also on the 4th urosomite of males, seems that has been evolved independently and a hypothetical ancestor with lateral windows in the fourth and fifth urosomites prior to the condition normally observed, with one lateral integumental window occurring only on the fifth urosomite, is not supported by the phylogeny (Fig. 7).

According to Martínez Arbizu and Moura (1994), all the Parastenocarididae share, as a synapomorphy, the loss of the inner seta on the basis of leg 1. However, the presence of this inner seta on both sexes of *R. ignotus* is an indication that this character is present in the groundpattern of the family and thus, should be considered as a plesiomorphy, since it also occurs in the sister group. The presence of this structure in other Parastenocarididae may be a homoplasy, but until now, it is impossible to know if it appeared several times or if it is present in the groundpattern of a more inclusive group outside *Remaneicaris*, being subsequently lost several times also within the family. Other structures, within the Parastenocarididae, have been or can be misinterpreted with a true inner spine. For example, an observation of *Murunducaris juneae* Reid, 1994 as well as some as yet undescribed species of *Murunducaris* Reid, 1994 revealed that there is a dimorphic inner spinule on the basis of the leg 1 of the males, with one small spinule on each side. We interpret this element not necessarily as a dimorphic spine or seta, like those found in the Ameiridae, since, in the female, in the same position, there is a row of three small spinules (the middle spinule is a little bigger than the others) and no seta at this position. There is no homology between spinule and spine or seta. The presence of a protrusion on the inner margin of the basis of leg 1 in the males of some species of *Parastenocaris* was hypothesized by Bruno and Cottarelli (1998) as being a possible homology with the true dimorphic spine observed on the inner margin of the basis of Ameiridae males. In accordance with Galassi and De Laurentiis (2004), this protrusion observed in some Parastenocarididae seems to be similar to a transformation of the inner margin of the basis that can be seen in several Diosaccidae Sars, 1906 and Thalestridae Sars, 1905 and is not homologous with the inner basal setae, since in most cases within these families, males show an inner protrusion accompanied by an untransformed seta.

Another very distinctive character of *Remaneicaris ignotus* is the presence of a proximal linear row of spinules on the outer margin of the first exopodite of leg 2 and leg 4. This character is

shared, as a plesiomorphy, with all other known Parastenocarididae outside *Remaneicaris*. Within *Remaneicaris* this character probably evolved in two steps, from linear until a pronounced “V” shaped distribution, passing through a moderate “v” condition.

The condition of leg 5 without intercoxal sclerite is a synapomorphy of *Remaneicaris*. The genus *Simplicaris* Galassi and De Laurentiis, 2004 is characterized by the loss of leg 5 and has, therefore, no intercoxal sclerite. However, it is difficult to know if other parastenocaridids have also lost the intercoxal sclerite because this character is seldom described. A sclerite connecting both limbs of leg 5 is present in both sexes of *Parastenocaris hispanica* Martínez Arbizu, 1997 for instance and can be seen also in *Murunducaris* as a hypertrophied plate.

The position of the leg 5 is another interesting feature of *R. ignotus*. In this species, these limbs are more ventrally located and not displaced to the ventro-lateral margins of the urosome, as can be seen in the other species within the genus. Thus, in view of the ventral position occupied by these limbs in other groups within the family and considering the basal position occupied by *R. ignotus* within the genus, hence, here we consider the presence of a more ventral leg 5 as a plesiomorphy within *Remaneicaris*.

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We would like to thank Dr. Danielle Defaye for the loan of the type material of *R. ignotus*. We thank the staff of the Deutsches Zentrum für Marine Biodiversitätsforschung (Forschungsinstitut Senckenberg) for their help during the permanence of the first author in Germany. This work is a part of the first author PhD Thesis and was supported by the Deutscher Akademischer Austausch Dienst (DAAD), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil), the Fundação de Amparo a Pesquisa do Estado do Amazonas (FAPEAM, Brazil) and the

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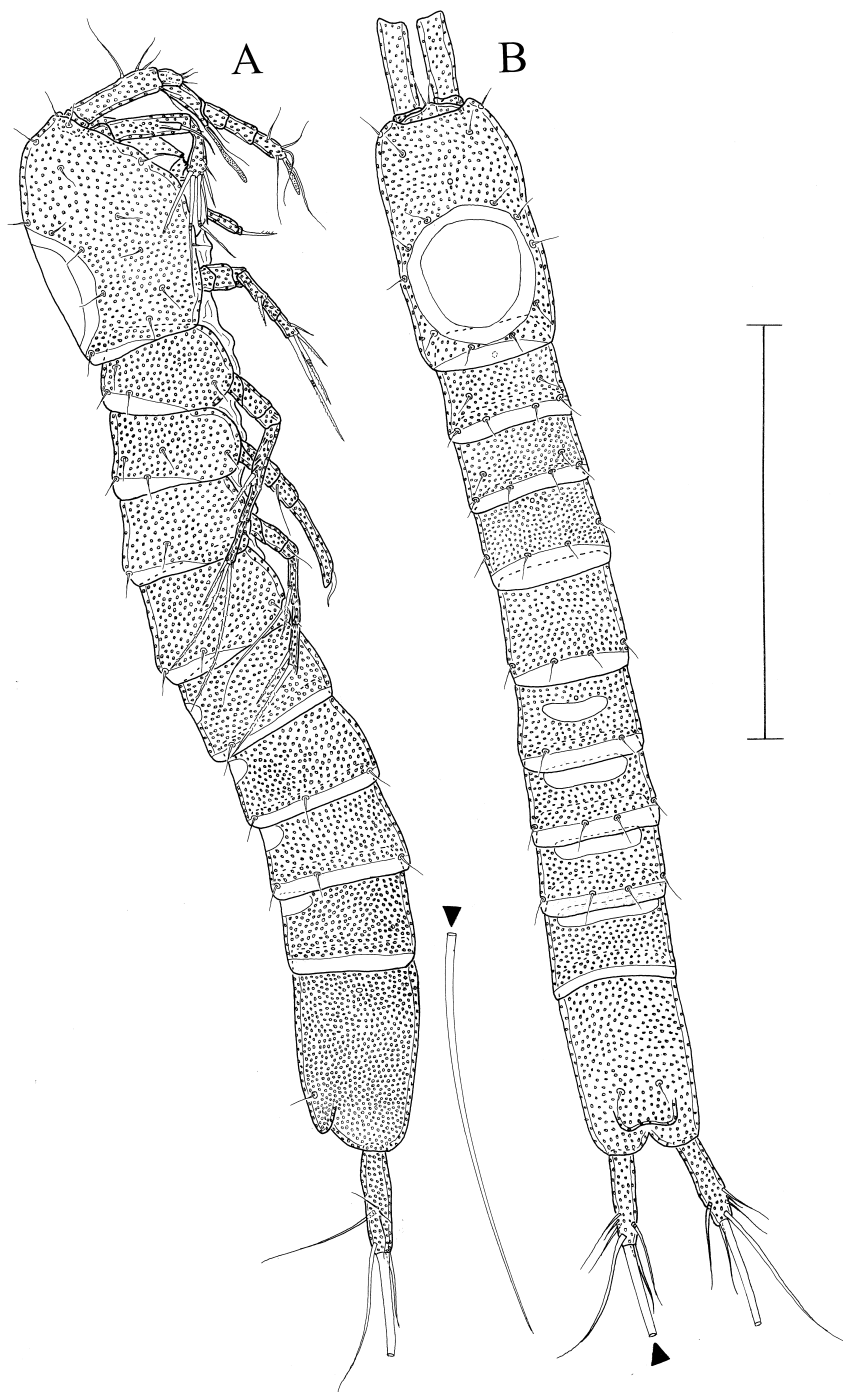


Figure 1- Male lateral lateral (A) and dorsal (B) habitus of *Remaneicaris ignotus* (Dussart, 1983). Scale bar= 100 μ m.

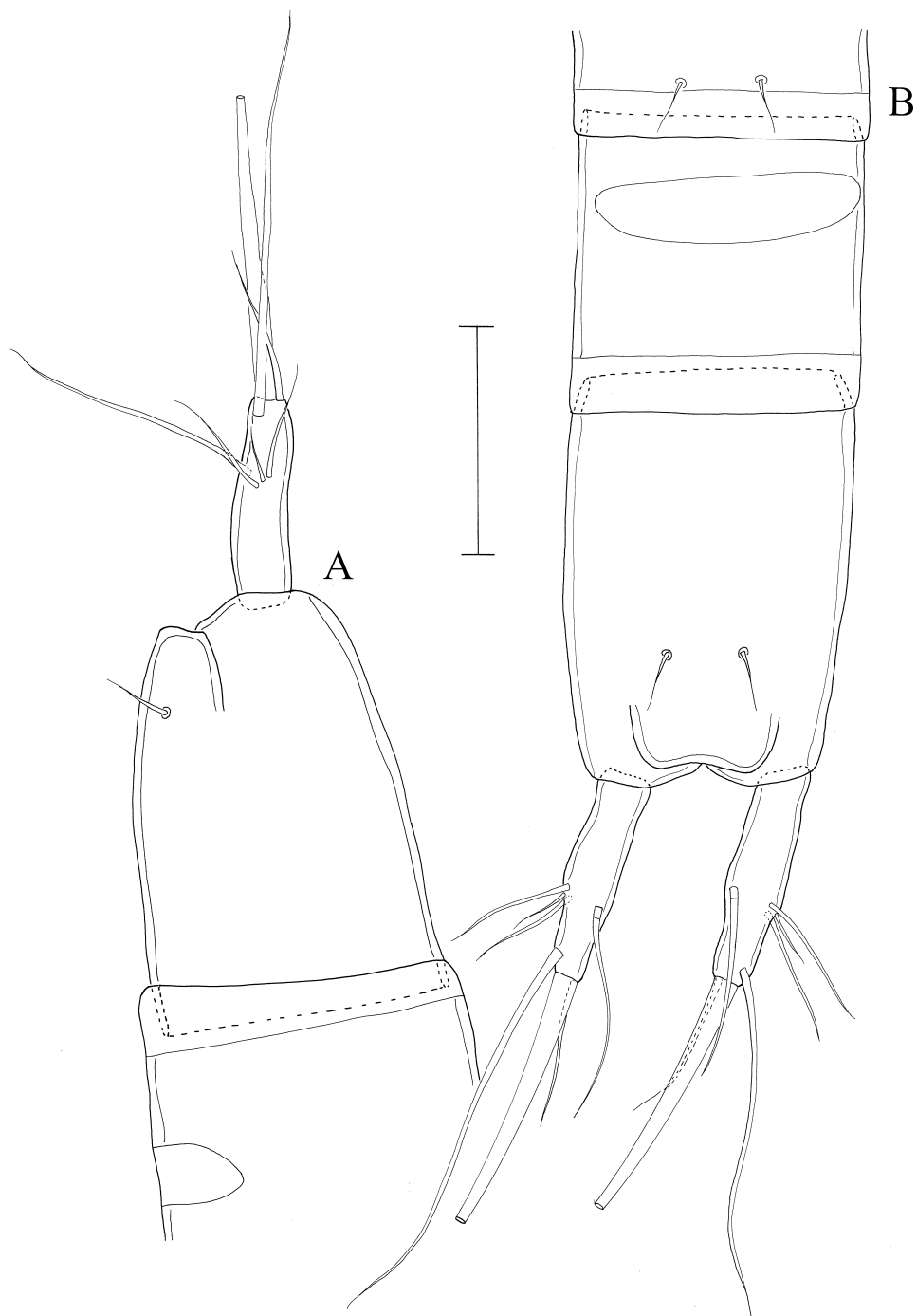


Figure 2- Male last urossomite and telson of *Remaneicaris ignotus* (Dussart, 1983) in lateral (A) and dorsal view (B). Scale bar= 25 μ m.

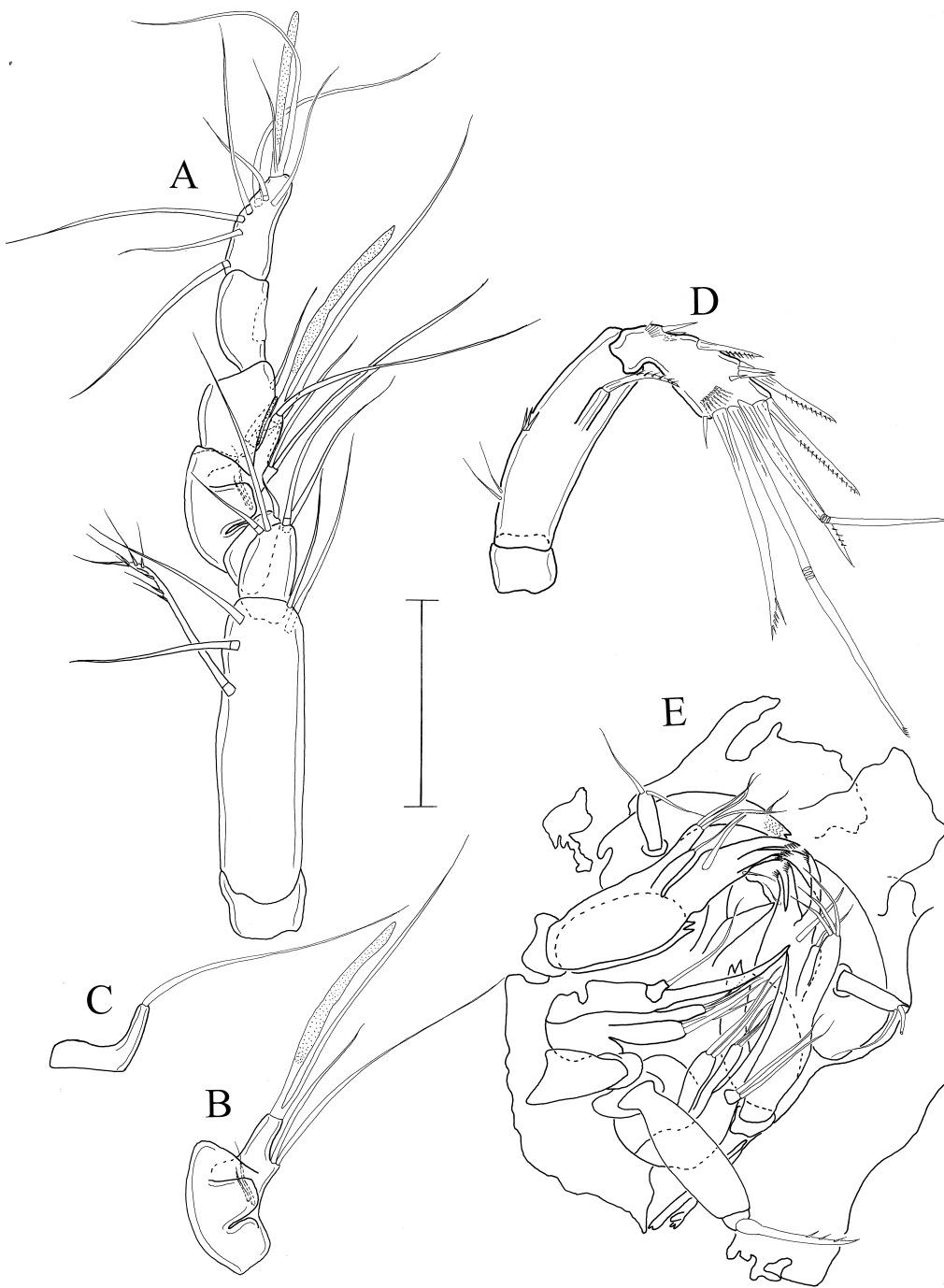


Figure 3- Male Antennule (A), 5th (B) and 6th (C) antennule segments, antenna (D) and bucal parts (E) of *Remaneicaris ignotus* (Dussart, 1983). Scale bar= 10 μ m.

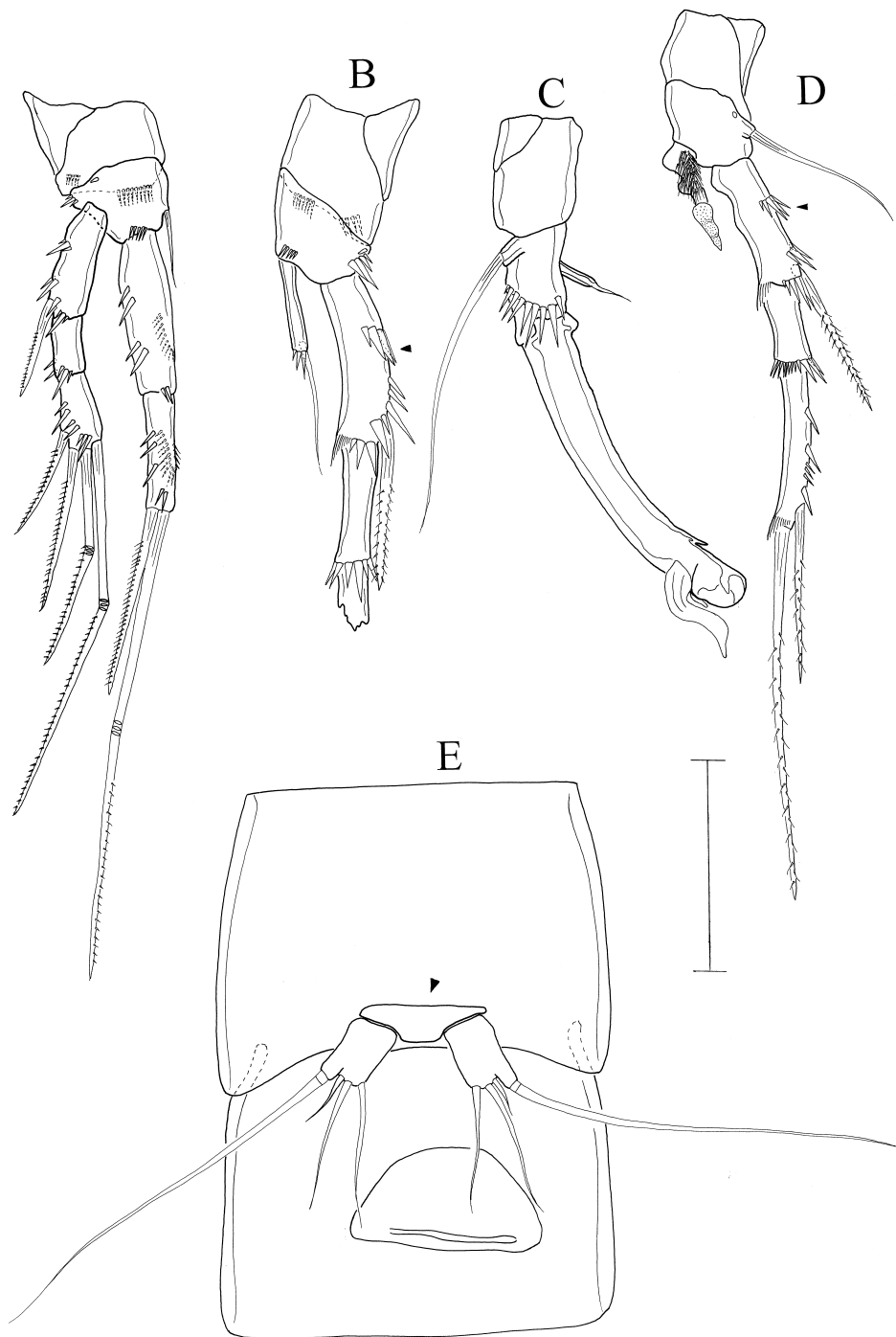


Figure 4- Male leg 1 (A), leg 2 (B), leg 3 (C), leg 4 (D) and leg 5 (E) of *Remaneicaris ignotus* (Dussart, 1983). Scale bar= 10 μ m. Arrows indicate the linear row of spinules on the outer margin of exp 1 of legs 2 and 4 and a low chitinized zone without any articulation with the leg 5.

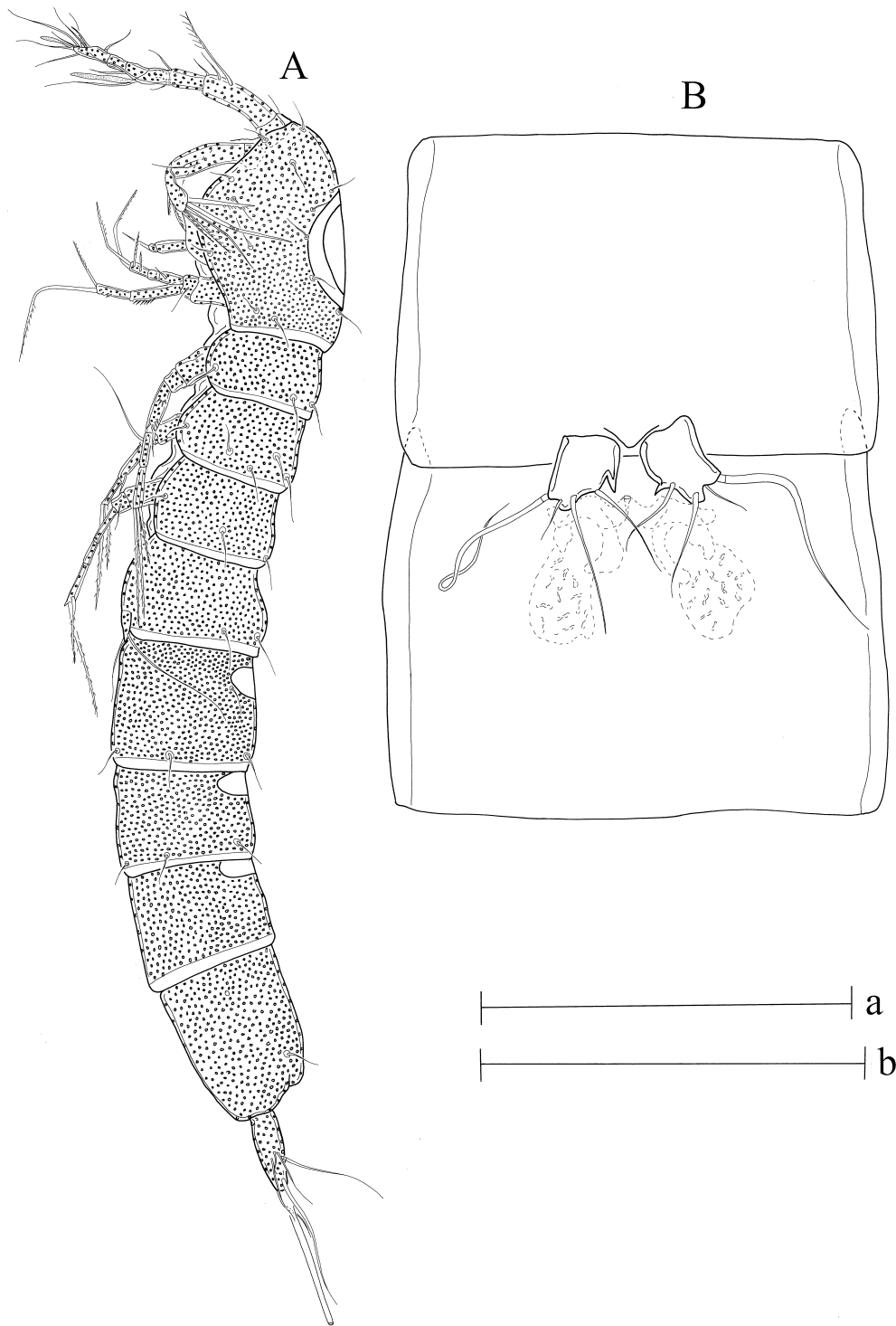


Figure 5- Female lateral habitus (A), leg 5 and genital somite (B) of *Remaneicaris ignotus* (Dussart, 1983). Scale bar a, for habitus=100 μm ; scale bar b, for ventral view of the first urosomite with leg 5 and double genital somite= 50 μm .

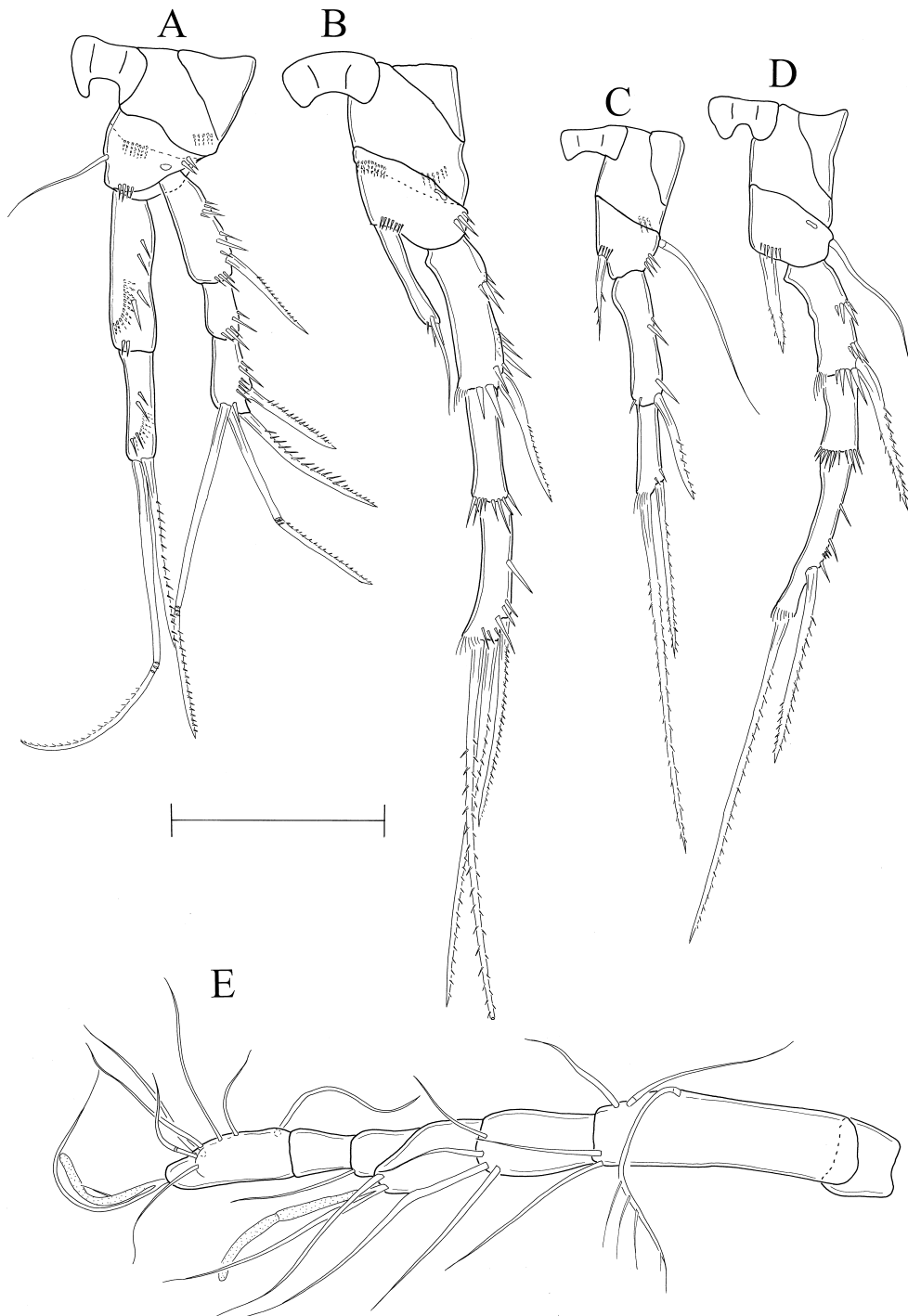


Figure 6- Female leg 1 (A), leg 2 (B), leg 3 (C), leg 4 (D) and antennule (E) of *Remaneicaris ignotus* (Dussart, 1983). Scale bar=20 μ m.

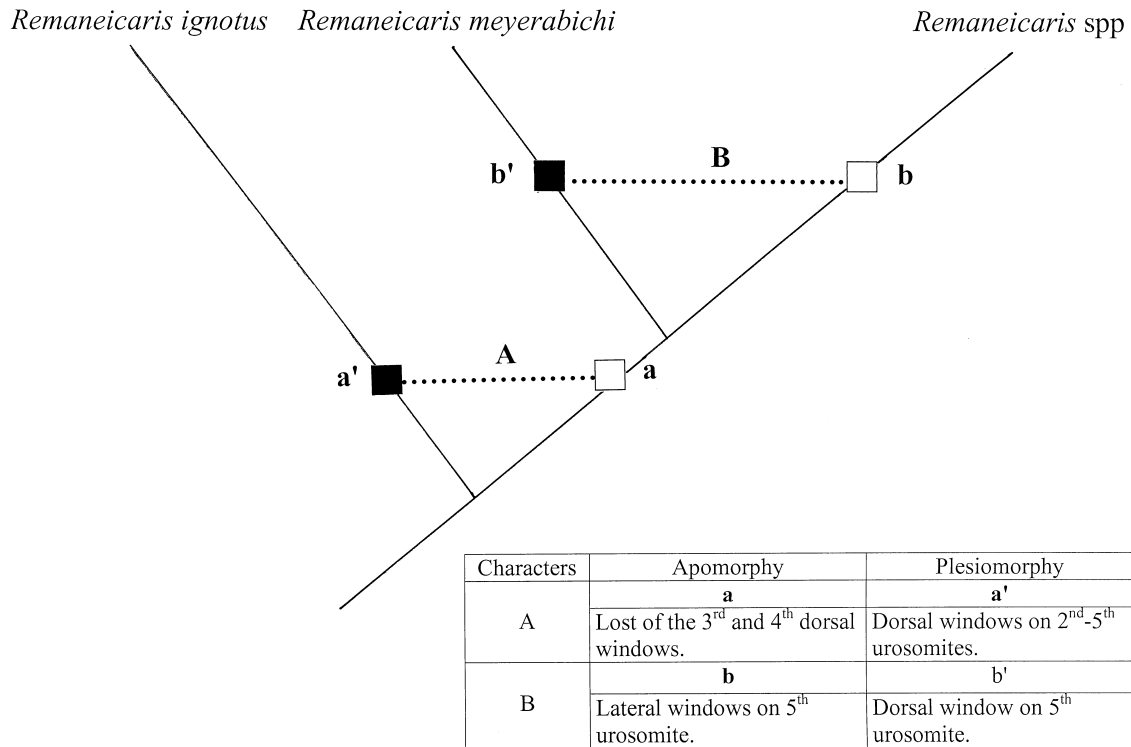


Figure 7- Schema of the phylogenetic relationship at the basis of *Remaneicaris* Jakobi, 1972 showing an hypothesis of how integumental windows patterns evolved within the genus. Small table with the characters (A and B) and character states (a and a'= apomorphy and plesiomorphy, respectively, for character A; b and b'= apomorphy and plesiomorphy, respectively, for character B. In females, there is a fusion between the 2nd and 3rd urosomites, with the formation of a double genital somite.

Chapter IV

Three new interstitial species of the *Remaneicaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae) closely related to the species around *R. analuizae* Corgosinho and Martínez Arbizu 2005

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Abstract

Three new species of *Remaneicaris* Jakobi of the “*analuizae*”-group, from southern and southeastern Brazil are described in detail. This is a typical *Remaneicaris* group, sharing with all its members the subdistal position of the seta of the exp 3 of leg 4. As an independent monophyletic group within *Remaneicaris*, the species from the “*analuizae*”-group share as a major synapomorphy, the presence of a hyaline margin on the distal edge of the 9th segment of the antennule in males. *Remaneicaris itacambirucui* n. sp., *R. insolitus* n. sp. and *R. ivoneae* n. sp. differ from each other by the number of integumental windows on the 2nd and 5th urosmites and by the ventral ornamentation of the proximal region of the telson, ventral ornamentation of the distal margin of the telson, ornamentation of the preoperculum, dorsal ornamentation of the telson, shape

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of the end of male leg 4 and leg 3, structure of the thumb and ornamentation of male leg 3. The evolution of each character is commented and their phylogenetic relevance is discussed.

Keywords: Copepoda, Parastenocarididae, *Remaneicaris*, hyporheos, Brazil.

Introduction

Created to group most of the species included by Noodt (1963) in the *remanei*-group, the genus *Remaneicaris* Jakobi, 1972 was not previously accepted by subsequent researches, due to the “Schalenmodell” system adopted by Jakobi (1972). The application of this methodology resulted in that some of the species previously placed by Noodt (1963, 1965) within the *remanei*-group (viz. *R. psammae* (Rouch, 1962), *R. hexacantha* (Kiefer, 1936) and *R. membranacea* (Noodt, 1965)), were subsequently excluded from it by Jakobi (1972), while others members from different evolutionary lineages, such as *Parastenocaris staheli* Menzel, 1916, *Murunducaris dactyloides* (Kiefer, 1967) and *P. itica* Noodt, 1962, were included by him within *Remaneicaris*.

This practice resulted in a polyphyletic group that, only recently (Corgosinho and Martínez Arbizu 2005), was recognized as a monophylum.

Nowadays, with 31 described species, the genus *Remaneicaris* Jakobi (1972) is the most diverse group of the Neotropical Parastenocarididae, occupying a basal position within the family (Corgosinho chapter 5). The genus is represented, until now, only by neotropical members. However, in the future, its distribution could be extended to Africa, if proved that *Parastenocaris ahaggarica* Bozic (1978) is a member of *Remaneicaris*, as presumed by Corgosinho (chapter 5).

Remaneicaris is very diverse in the southern of South America, and can be splitted in at least five monophyletic groups (Corgosinho chapter 5), being them composed by species related to *R. argentina* (Noodt, 1965), *R. analuizae* Corgosinho and Martínez Arbizu, 2005, *R. tridactyla* Corgosinho, Martínez Arbizu and Santos Silva, 2007, *R. persephone* (Noodt, 1965) and *R.*

cordobaensis (Noodt, 1965). The most diverse group, a taxon composed by a complex of species related to *R. persephone* and *R. cordobaensis* seems to be endemic to Argentina. Probably its eastern and western limits are the Paraná River and the Andinean mountain range respectively. Other groups such as the “*tridactyla*” and “*argentina*” groups have a more widespread distribution.

The “*analuizae*”-group seems to be especially diverse in the southeastern and southern of Brazil. It can be easily characterized by the presence of a hyaline margin on the distal edge of the 9th segment of the antennule in males. This group occurs in Minas Gerais as well as in Atlantic coastal rivers and in the proximity of the Paraná River (in the Brazilian shield). Albeit of its broad distribution, the geographical range is not yet well understood and only four species are known. However, its occurrence in the hydrographical basins' of the São Francisco, Paraná and Jequitinhonha rivers can reveal, in the future, a very diverse group with one of the widest distribution in South America.

In this paper we describe three new species of *Remaneicaris* from the “*analuizae*”-group. Additionally, the evolution of each character is commented and their phylogenetic relevance is discussed.

Material and Methods

The samples were taken next to the river bank using the Karaman-Chappuis method (Chappuis 1942) using a 100 µm mesh, stained with rose bengal, and fixed with formalin at a final concentration of about 4%. Animals were dissected in lactic acid and mounted on slides in glycerine. Drawings were made using a drawing tube on a Leica DMR microscope, equipped with Normarsky interference contrast, at 400x and 1000x magnification.

Abbreviations used are: A1 = antennule, A2 = antenna, Ae = aesthetasc, Md = mandible, Mx1 = Maxillulae, Mx2 = Maxillae, Mxp = maxilliped, enp = endopod, exp = exopod. The type

material is deposited in the invertebrate collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Descriptive part

Family Parastenocarididae Chappuis, 1940

Genus *Remaneicaris* Jakobi, 1972

***Remaneicaris insolitus* n. sp.**

Type material: Holotype, one dissected male on 7 slides (INPA 1451 a-g).

Derivatio nominis: The term *insolitus*, from Latin means unusual, uncommon, strange.

Locus typicus: The type material was taken in a small stream localized behind the "Hotel Fazenda Fonte Colina Verde", at the city of São Pedro (State of São Paulo, Brazil).

Male. Habitus (Fig. 1 A-B). Length 310µm (measured from tip of rostrum to distal rim of anal operculum). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax with 1 dorsal integumental window (Fig. 1A-B). Second urosomite with a dorsolateral window on each side of the somite (Fig. 1B and 2B). Last urosomite with two small dorsolateral windows on each side of the somite (Fig. 1A-B; 2A-B). For sensilla on tergites see Fig. 1 A-B. Proximal region of the telson with 1 continuous row of spinules that reaches, laterally, the proximal third of the segment; near the insertion of the furca, with a ventral row of up to 7 spinules (Fig. 2 A-B). Operculum convex, without ornamentation and flanked with 2 spinules on each side, on the paraopercular margin (Fig 1B and 2 A). Furca (Fig. 2 A-B) with 7 setae; all setae located on the distal third; setae I, II and III inserted at the same level of seta VII; distoventral margin with 2 spinules. A1 9-segmented, geniculated and with a peculiar hyaline tip on the distal segment; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/3/2/9+Ae. A2 with allobasis, 1-

segmented exp with 1 seta, and 1-segmented enp bearing a ventral hyaline frill and 7 setae. Md, Mx1, Mx2 and Mxp armature as in *Remaneicaris analuizae* Corgosinho and Martínez Arbizu, 2005.

Leg 1 (Fig. 3 A) coxa unarmed, with one row of spinules on the posterior side; basis with outer seta, 3 spinules on outer margin and 1 pore on anterior margin; distally, with two spinules between the exp and the enp; inner margin with a bare protuberance; exp 3-segmented, segment 1 with outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae; enp 2-segmented, segment 1 with 1 row of 3 long spinules along inner margin and 2 rows of spinules on outer margin; segment 2 with one distal spine, a geniculated seta and a row of spinules along the inner and outer margins. Leg 2 (Fig. 3 B) coxa unarmed, with 1 row of small spinules on the posterior margin; basis without outer seta, with an anterior pore, one row of spinules on the outer margin and 5 spinules near the insertion of the enp; exp 3-segmented, the first segment approximately of the same size as the remaining segments combined, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of an outer spine and an inner hyaline frill, segment 2 without armature, with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size, segment 3 with 3 setae a, distal hyaline frill on the inner corner, and two spinules located mesially on the outer margin; enp 1-segmented with 1 subdistal seta, 3 distal spinules, and 4 spinules along the outer margin. Leg 3 (Fig. 3 C) coxa unarmed, with a posterior row of spinules; basis with outer seta, one anterior pore and ornamented with three spinules on the outer margin, between the outer seta and the insertion of the exp; enp 1-segmented, oval and with a row of spinules on the distal margin; exp 1-segmented, elongated, almost straight, ornamented with a series of spinules along the entire outer margin; thumb straight, forming an angle of 90° with the main axis; apophysis short and rounded. Leg 4 (Fig. 3 D) coxa unarmed, with a posterior row of spinules; basis with outer seta (not observed in the figure 4 D) and one pore on the anterior margin; exp 3-segmented, the first segment approximately of the same size as the remaining segments

combined, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of the outer spine and a inner hyaline frill, segment 2 without armature, with two spinules located mesially on the outer margin, an inner row of spinules and a row of distal spinules of unequal size (innermost smaller than outermost), segment 3 with 3 setae, a distal hyaline frill on the inner corner, and three spinules located mesially, on the outer margin; enp 1-segmented, leaf-shaped, covered with numerous long spinules along the inner margin, not ornamented on the outer margin. Leg 5 (Fig. 3 E) relatively big, almost trapezoidal, with a distal spinulous process on the inner margin and with all setae inserted on the outer margin.

***Remaneicaris itacambirucui* n. sp.**

Type material. Holotype: 1 male, dissected and mounted on 7 slides (INPA 1452 a-g).

Derivatio nominis: The species name refers to the Itacambiruçu River, on the Basin of Jequitinhonha River, in the state of Minas Gerais, Brazil.

Locus typicus: Itacambiruçu River, state of Minas Gerais, Brazil. Coordinates: 16°35'34"S 42°55'15"W.

Male habitus. Length 325µm (measured from tip of rostrum to distal rim of anal operculum).

Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax and second urosomite with 1 dorsal integumental window. Last urosomite with one lateral integumental window on each somite. Telson with a row of up to 5 spinules on the distal third of the segment before the sensilla; operculum smooth and convex; preopercular zone ornamented with 3 spinules of unequal size (the middle one bigger than the others); ventrally with a row of 5 spinules on each side near the insertion of the furca. Furca as in *Remaneicaris insolitus* n. sp., with 7 setae, all of them located on the distal third; setae I, II and III inserted at the same level of seta VII; distoventral

margin with 2 spinules. A1 9-segmented, geniculated and with a peculiar hyaline tip on the distal segment; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/3/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing a ventral hyaline frill and 7 setae. Md, Mx1, Mx2 and Mxp armature of the *Remaneiacaris* type, as in *R. insolitus* n. sp. Leg 1 coxa unarmed; basis with outer seta, 2 spinules on the outer margin and 1 pore on outer margin; exp 3-segmented, segment 1 with outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae; enp 2-segmented, segment 1 with 1 row of 5 long spinules along inner margin and 2 rows of spinules on the outer margin; segment 2 with one spine, a geniculated seta and a row of spinules along the inner and outer margin. Leg 2 coxa unarmed, with 1 row of small spinules on the posterior margin; basis without outer seta, with 1 row of spinules on the outer margin, an anterior pore and a row of spinules distally, near the insertion of the enp; exp 3-segmented, the first segment approximately of the same size of the remaining exp, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of an outer spine and an inner hyaline frill, segment 2 without armature, with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size, segment 3 with 3 setae, a distal hyaline frill on the inner corner, and one spinules located mesially on the outer margin; enp 1-segmented with 1 distal seta, 2 distal spinules, and 3 spinules along the outer margin. Leg 3 (Fig. 4 B) coxa unarmed; basis with outer seta; enp 1-segmented, with a distal seta and 2 distal spinules; exp 1-segmented, elongated, almost straight, ornamented with a series of spinules along the entire outer margin; the distalmost spinules are very long; thumb curved with a hyaline inner margin; apophysis is bigger than the thumb, inwardly curved and with a rounded tip. Leg 4 (Fig. 4 A) coxa unarmed, with a posterior row of spinules; basis with outer seta and one pore on the outer margin; exp 3-segmented, the first segment approximately of the same size as the remaining exp, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of the outer spine and

an inner hyaline frill, segment 2 without armature, with one spinule located mesially on the outer margin, an inner row of spinules and a row of distal spinules of unequal size (innermost smaller than outermost), segment 3 with 3 setae, a distal hyaline frill on the inner corner, and two spinules located mesially, along the outer margin; enp 1-segmented, short, leaf-shaped, covered with numerous long spinules on the inner margin, not ornamented on the outer margin. Leg 5 with a distal spinulous process on the inner margin and with all setae inserted on the outer margin.

***Remaneicaris ivoneae* n. sp.**

Type material. Holotype: 1 male, dissected and mounted on 7 slides (INPA 1453 a-g).

Derivatio nominis: The species is named after the senior author's aunt, Ivone Corgosinho Baumecker.

Locus typicus: Nhundiaquara River, state of Paraná, Brazil. Coordinates: 25°28'41"S 48°49'37"W.

Male habitus. Length 280µm (measured from tip of rostrum to distal rim of anal operculum).

Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax and second urosomite with 1 dorsal integumental window. Last urosomite with one lateral integumental window on each side. Telson smooth on the dorsal side, ventrally with a row of four small spinules on each side of the somite, near the insertion of the furca; operculum smooth and convex. Furca with 7 setae; all setae located in the distal third; setae I, II and III inserted at the same level of seta VII; distoventral margin with 2 spinules; dorsally with two spinules on the distal third of the furca. A1 9-segmented, geniculated and with a peculiar hyaline tip on the distal segment; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/3/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing a ventral hyaline frill and 7 setae. Md, Mx1, Mx2 and Mxp armature as in *R. insolitus* n. sp. Leg 1 (Fig. 5 A) coxa unarmed; basis with outer seta and 1

pore on anterior outer margin, 2 spinules on the outer margin and one spinule near the insertion of the enp; exp 3-segmented, segment 1 with outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae; enp 2-segmented, segment 1 with 2 long spinules along inner margin and 2 rows of spinules on the outer margin; segment 2 with one spine, a geniculated seta and a row of spinules on the outer margin. Leg 2 (Fig. 5 B) coxa unarmed; basis without outer seta, ornamented with 1 row of spinules on the outer margin and a row of spinules distally, near the insertion of the enp; exp 3-segmented, the first segment approximately as the same size of the remaining exp, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of an outer spine and an inner hyaline frill, segment 2 without armature, with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size, segment 3 with 3 setae, a distal hyaline frill on the inner corner, and one spinule located mesially on the outer margin; enp 1-segmented with 1 distal seta, 2 distal spinules, and 2 spinules along the outer margin. Leg 3 (Fig. 5 C) coxa unarmed, with a posterior row of spinules; basis with outer seta, an outer pore, one row of spinules near the outer pore and 2 spinules on the inner margin; enp 1-segmented, batoniform, without armature or ornamentation; exp 1-segmented, elongated, almost straight, ornamented with a series of spinules along the entire outer margin; thumb straight, with a hyaline inner margin; apophysis short and rounded. Leg 4 (Fig. 5 D) coxa unarmed, with a posterior row of spinules; basis with outer seta and one pore on the anterior outer margin; exp 3-segmented, the first segment approximately of the same size as the remaining exp, with a proximal row of spinules distributed in a “V” shape, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill, segment 2 without armature, with one spinule located mesially on the outer margin, an inner row of spinules and a row of distal spinules of unequal size (innermost smaller than outermost), segment 3 with 3 setae, a distal hyaline frill on the inner corner, and one spinule located mesially, on the outer margin; enp 1-segmented, filiform, covered with three long

spinules on the proximal third of the inner margin and a row of very small spinules covering the distal portion of the inner margin, enp. not ornamented on the outer margin. Leg 5 (Fig. 5 E) with a distal spinulose process on the inner margin and with all setae inserted on the outer margin.

Discussion

The three species described here belong to a bigger group within *Remaneicaris* that has, as an autapomorphy, an inner row of spinules on the exp 2 of leg 4 and the proximal outer row of spinules on the exp 1 of leg 4 distributed as a pronounced V (Corgosinho chapter 5). The first character appears also in other species outside *Remaneicaris*, but it seems restricted to some unrelated species within “Fontinalicaridinae”. However, the V-shaped row of spinules on the antero-outermost margin of leg 4 exp 1, to our knowledge, appears only within *Remaneicaris*.

Most of the *Remaneicaris* species described until now (23 species) share the synapomorphies mentioned on the paragraph above. Within this big monophyletic group we can see two clear evolutionary tendencies, easily identified on the basis of the structure of the last segment of the A1 of males and the ornamentation of the basis of male's leg 4 (Corgosinho chapter 5). The most speciose group, composed by the “*tridactyla*”, “*peresePHONE*” and “*cordobaensis*” groups is characterized by the presence, in males, of a row of spinules on the inner margin of the basis of leg 4, as well as a row of spinules near the insertion of the endopod, in a low cuticularized area and a modified seta on the last segment of the A1 of males. The species described here do not have such characters, being characterized by the presence of a hyaline margin on the distal rim of the 9th segment of males A1. No other species within *Remaneicaris*, outside the “*analuiZae*” group, or even within the whole family have such character.

Remaneicaris itacambirucui n. sp., *R. insolitus* n. sp. and *R. ivoneae* n. sp. differ from each other in the number of integumental windows on the 2nd and 5th urosmites (2nd and 4th on the

females), ventral ornamentation of the proximal region of the telson, ventral ornamentation of the distal margin of the telson, ornamentation of the preoperculum, dorsal ornamentation of the telson, shape of the emp of male leg 4 and leg 3, structure of the thumb and shape and ornamentation of male leg 3.

Remaneicaris itacambirucui n. sp. seems to be closely related to *R. ivoneae* n. sp., with whom it shares the presence of a hyaline inner margin on the thumb. However, the presence of a hyaline structure on the thumb can be seen also in *R. paraensis* (Noodt, 1963), *R. paraguayensis* (Noodt, 1963) and *R. hecate* (Nodt, 1965). This is one of the most homoplastic characters within the genus, appearing four times in three different monophyletic groups. Thus, in the absence of more enlightening characters, the exact phylogenetic position of both species within the *analuizae*-group is difficult to determine.

Number, presence and shape of the integumental windows within Parastenocarididae have been a matter of controversy (i.e. Reid 1994, Corgosinho and Martínez Arbizu 2005). Most of the original descriptions lack the illustration of these structures, thus making difficult the interpretation of the evolution of this character without the observation of the types. For example, in *Remaneicaris*, the presence, position and number of these structures have been of great importance for the reconstruction of the phylogeny of the group (Corgosinho chapter 5). In accordance with Corgosinho and Martínez Arbizu (2005), a complex series of transformation should be involved, with a gradual modification of the position, shape and presence of this structure in different urosomites. However, with the data at hand, the scenario is not so complex as proposed before, being involved, in this case (considering only the males), the loss of the dorsal integumental window of the 3rd and 4th urosomites, the splitting and lateral migration of the integumental window of the 5th urosomite and then, the split, in two dorsolateral windows, of the dorsal integumental window present on the 2nd urosomite. Other patterns such as the presence of a lateral

integumental window on the 4th urosomite of the male, as observed in *R. analuizae*, until now, should be considered as a reversion or independent evolution (Corgosinho chapter 5). As an example of a situation that could make difficult the reconstruction of the phylogeny of *Remaneicaris*, we can mention the last transformation suffered by the integumental window of the 2nd urosomite of the “*persephone*”-group. In Noodt’s original description (Noodt 1965), this author did not draw or even mentioned the splitting of the dorsal integumental window, of the 2nd urosomite, in two parts. However, this is a synapomorphy for a monophyletic group formed by *R. oncophora* (Noodt, 1965), *R. pluto* (Noodt, 1965), *R. hecate*, *R. persephone* (Noodt, 1965), *R. rhizophora* (Noodt, 1965) and *R. membranacea* (Noodt, 1965). The same character appears also in *R. insolitus* n. sp. In this species, however, it is a clear homoplasy, appearing within the groups “*persephone*” and “*analuizae*” independently (Corgosinho chapter 5). Additionally, *R. insolitus* n. sp. can be easily identified and distinguished from the other species from the same locus typicus by the presence of a double lateral integumental window on each side of the 5th urosomite. This is a very peculiar character not seen before even within the family. However, the observation of more material can reveal, in the future, some other species with this kind of structure within *Remaneicaris*.

Ornamentation of the telson is also a very variable character within the genus *Remaneicaris*. It is more developed within the “*tridactyla*”-group (viz. Corgosinho et. al 2007; Corgosinho chapter 5; Corgosinho *et al.* chapter 6), but can also be found in other parastenocaridids. In the “*tridactyla*”-group it appears as a dorso-distal (DRS) row of spinules located directly before to the sensilla, a proximal row of spinules also on the dorsal side of the telson and a well developed row of spinules on the ventral side, near the insertion of the furca. Other species from different monophyletic groups within *Remaneicaris* also display these characters, probably as a consequence of convergent evolution (Corgosinho chapter 5). For example, within the “*analuizae*”-group, only *R.*

itacambirucui n. sp. has a DRS, while inside other monophyla, *R. ciliata* (Noodt, 1965), *R. sierrae* (Noodt, 1965) and *R. persephone* also have this character (Corgosinho chapter 5).

The presence of preopercular ornamentation is one of the synapomorphies of the “*analuizae*”-group (Corgosinho chapter 5). Within this group, only *R. ivonae* n. sp. does not display such structure, probably as a consequence of a secondary loss. Inside the genus *Remaneicaris*, this character can be observed also in *R. paraensis*, in the “*tridactyla*”-group. Also *Parastenocaris mateusi* Noodt and Galhano, 1969, *P. spinicauda* Wells, 1964 and *P. bolbodes* Kiefer, 1968, display such character. However, *Parastenocaris mateusi* and *P. spinicauda* clearly belong to the subfamily “Parastenocaridinae” (Schminke 1993), being easily characterized by the presence of an outer process on the penultimate segment of the A1 of the males, while *P. bolbodes* seems to be a member of the subfamily “Fontinalicaridinae” (Schminke 1993). The phylogenetic reconstruction of the family Parastenocarididae is far from completion. Until now is even difficult to define the monophyletic groups within the family and even more difficult to define degrees of kinship between species and groups of species. However, there is no doubt that that this character appeared independently within different and not closely related groups of Parastenocarididae.

In *R. insolitus* n. sp., the presence of a continuous row of spinules on the proximal region of the ventral side of the telson is considered a synapomorphy for a taxon formed by *R. insolitus* sp. nov and *R. divae* (Noodt, 1972). *Remaneicaris tageae* (Noodt, 1972), *R. euniceae* Corgosinho and Martínez Arbizu, 2005 and *R. analuizae* also have some ornamentation on the proximal region of the ventral side of the telson. However, in these species, this ornamentation is not formed by a continuous row of spinules, but it is represented by one small row of spinules on each side of the telson. In accordance with Corgosinho (chapter 5), the most parsimonious assumption is to consider both ornamentation as appearing independently within the “*analuizae*”-group.

Shape of leg 4 enp is an extremely variable character within the family Parastenocarididae. Jakobi (1972) used this variability to justify the creation of 26 new genera, while in the past; other authors (viz. Chappuis 1937, Kunz 1938 and Lang 1948) used the structure of the whole leg 4 and mainly of the enp as a basis for the creation of different groups within the family. In the Neotropis we can observe different evolutionary tendencies. For example, the most transformed leg 4 enp is observed in the genera *Forficatocaris* Jakobi, 1972 and *Potamocaris* Dussart, 1970. In these genera, the enp is somehow hypertrophic and well chitinized, while in the genus *Siolicaris* (Jakobi, 1972), the enp is extremely reduced or absent. All *Remaneicaris* species have a well developed enp on the leg 4 of males. However, the degree of development and of ornamentation is very variable, resulting in at least two morphological patterns, with an unclear phylogenetic value within the genus. We can mention, for example, the presence of a short enp with spinules on the outer margin, common in the “argentina”-group and also in the “cordobaensis”-group. Another pattern is the longer, leaf shaped and hirsute enp of the groups “anluizae” and “tridactyla”. In *Remaneicaris insolitus* n. sp. and *R. itacambirucui* n. sp. the enp is of the leaf shaped type, while in *R. ivoneae* n. sp., the enp is long, less ornamented, with three long spinules on the inner margin and ending in a seta incorporated to the segment. We interpret this as a modification of the hirsute type present in the “analuizae”-group .

The presence of a low cuticularized region on the basis of the leg 4 of the male, near the insertion of the enp is an interesting character of *R. insolitus* n. sp. Until now, this structure have been observed only in the groundpattern, as an autapomorphy of a bigger monophylum formed by the “tridactyla”, “persephone” and “cordobaensis” groups (Corgosinho chapter 5). These groups have as one of their most important synapomorphies the presence of a modified seta on the last segment of the A1 of males (Corgosinho chapter 5). *Remaneicaris insolitus* n. sp., however, belong to the “analuizae”-group, being well characterized, as already mentioned, by the presence of a

hyaline structure on the distal rim of the last segment of male A1. Considering this, and in the view of the absence, in the other species within the “*analuizae*”-group, of a low cuticularized region on the basis of the leg 4 of males, thus, the most parsimonious hypothesis is to consider this structure as a homoplasy.

Another very variable, but informative character within the family is the structure of the male leg 3. The usefulness of this limb for the reconstruction of the phylogeny of Parastenocarididae and definition of monophyletic groups can be seen in the recent literature. For example, in accordance with Corgosinho (chapter 5), the presence of an enp on male leg 3 is a plesiomorphy of the genus *Remaneicaris*, being its absence, a synapomorphy of the remaining Parastenocarididae. Martínez Arbizu (1997) used some characters from male leg 3 to define the *fontinalis*-group. Ahnert (1994) used the presence of an inner process (“Innerandvorsprung”) on the basis of this appendix (not adopted by Martínez Arbizu (in. prep)), as a synapomorphy for a taxon formed by *Forficatocaris* and *Potamocaris*. Recently, Corgosinho *et al.* (in prep.) recognized the genus *Brasilibathynellocaris* Jakobi, 1972 and proposed a new diagnosis for it, also based on the structure of the leg 4 of males. Also within *Remaneicaris*, the structure of the leg 3 of males has been of considerable importance for the resolution of the phylogeny within the genus. In this sense, Corgosinho (chapter 5) used the presence of a hyaline apophysis and the presence of a modified distal spinule on the outer margin of the exp of male leg 3, as an autapomorphy of the “*argentina*”-group. Beyond these clear tendencies, the general shape and structure of male leg 3 can vary considerably between two or more monophyletic groups or even within one given monophylum. For example, within the same monophylum *R. euniceae* and *R. analuizae* have an enp reduced to small setae, while the other species within this group have a well developed and 1-segmented enp. In almost all species in this group, male leg 3 is represented by a straight exp, ornamented with a continuous row of spinules along the outer margin (viz. *R. insolitus* n. sp., *R.*

ivoneae n. sp., *R. itacambirucui* n. sp., *R. tageae* and *R. divae*). A variable pattern can be seen in *R. itacambirucui* n. sp., where the distal portion of the outer row of spinules is represented by very long spinules. Only in *R. euniceae*, the exp is slightly inward curved, as a consequence of a proximo-medial bent. In *R. itacambirucui* n. sp. a similar pattern is achieved as a consequence of apophysis growth. Albeit of the variability found within *Remaneicaris*, we could say, with a good degree of certainty, that the presence of a straight exp on male leg 3 is a plesiomorphy of the genus.

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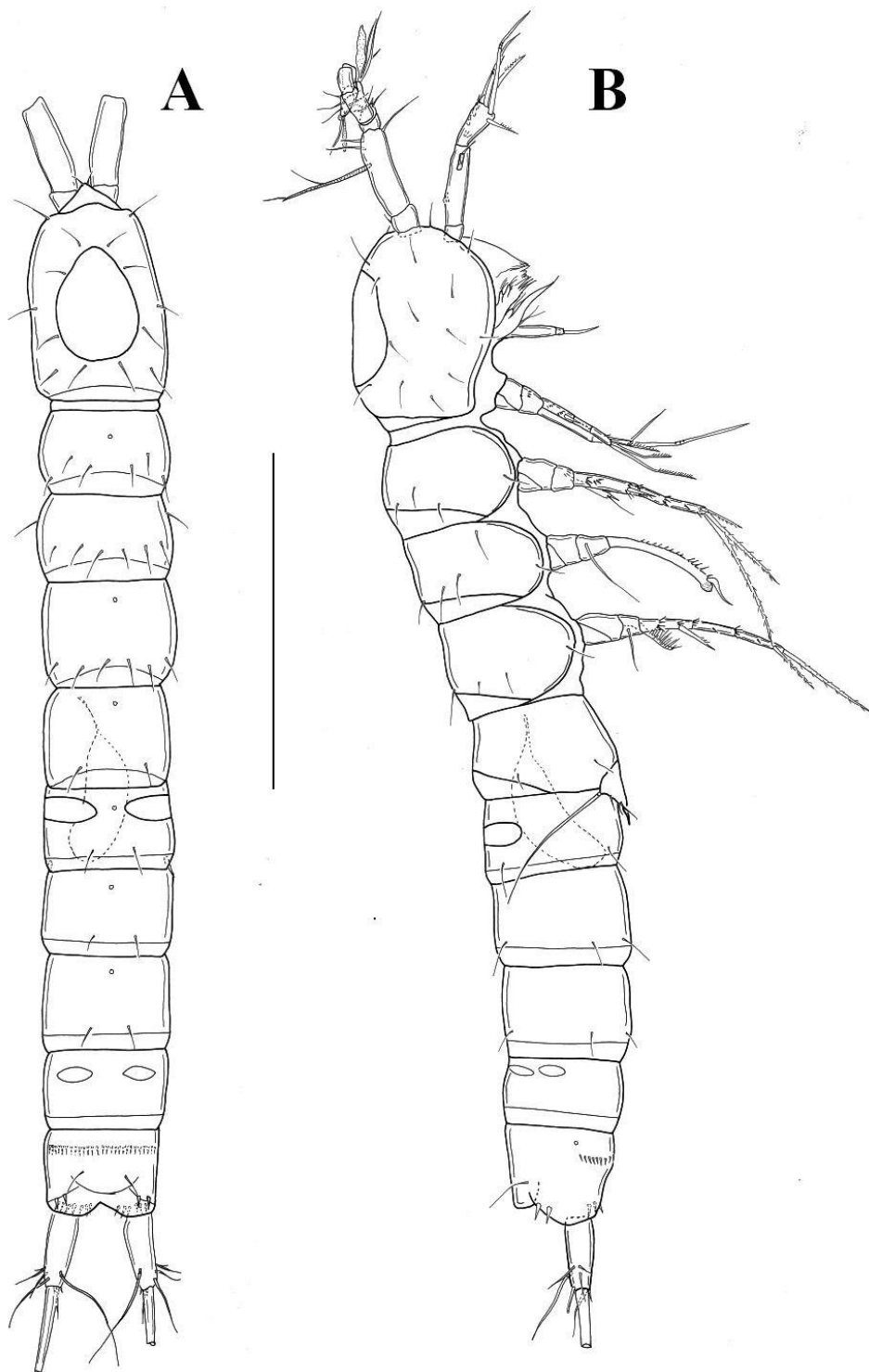


Figure 01- *Remaneicaris insolitus* n. sp., male. A, habitus, dorsal view; B, habitus, lateral view. Scale bar= 100 μ m

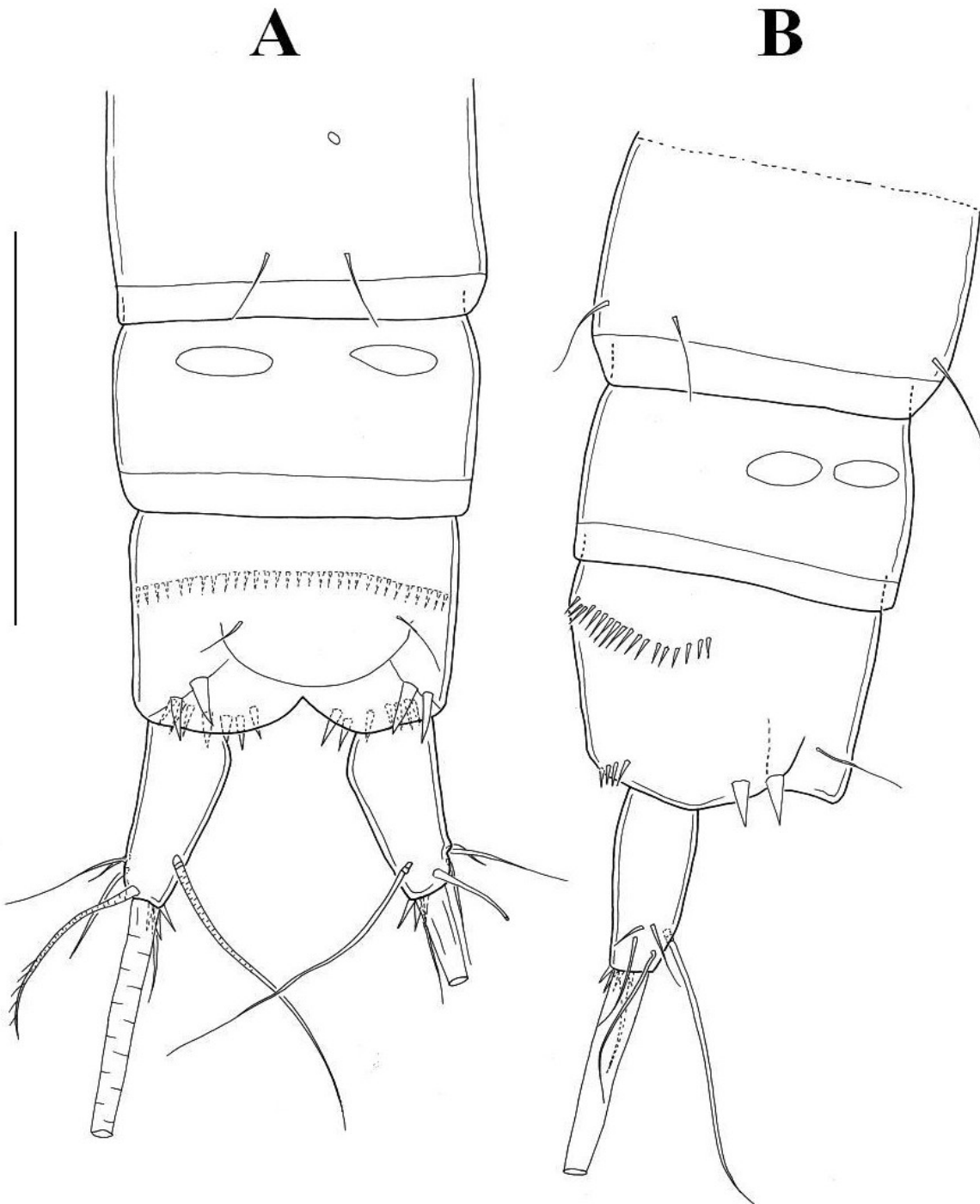


Figure 02- *Remaneicaris insolitus* n. sp., male. Last abdominal somite and telson. A, dorsal view; B, lateral view. Scale bar= 50 μ m

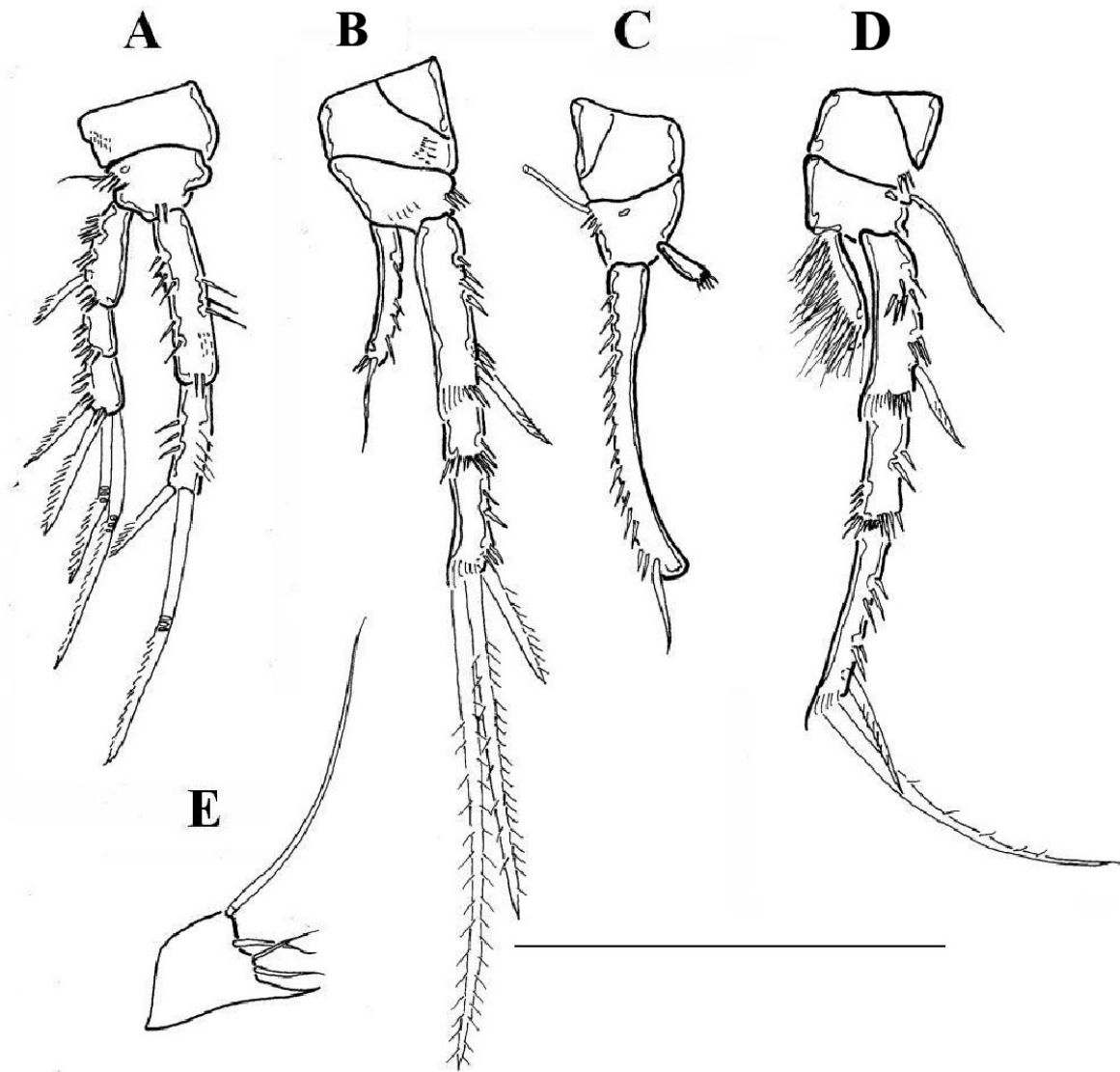


Figure 03- *Remaneicaris insolitus* n. sp., male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar= 50 μ m

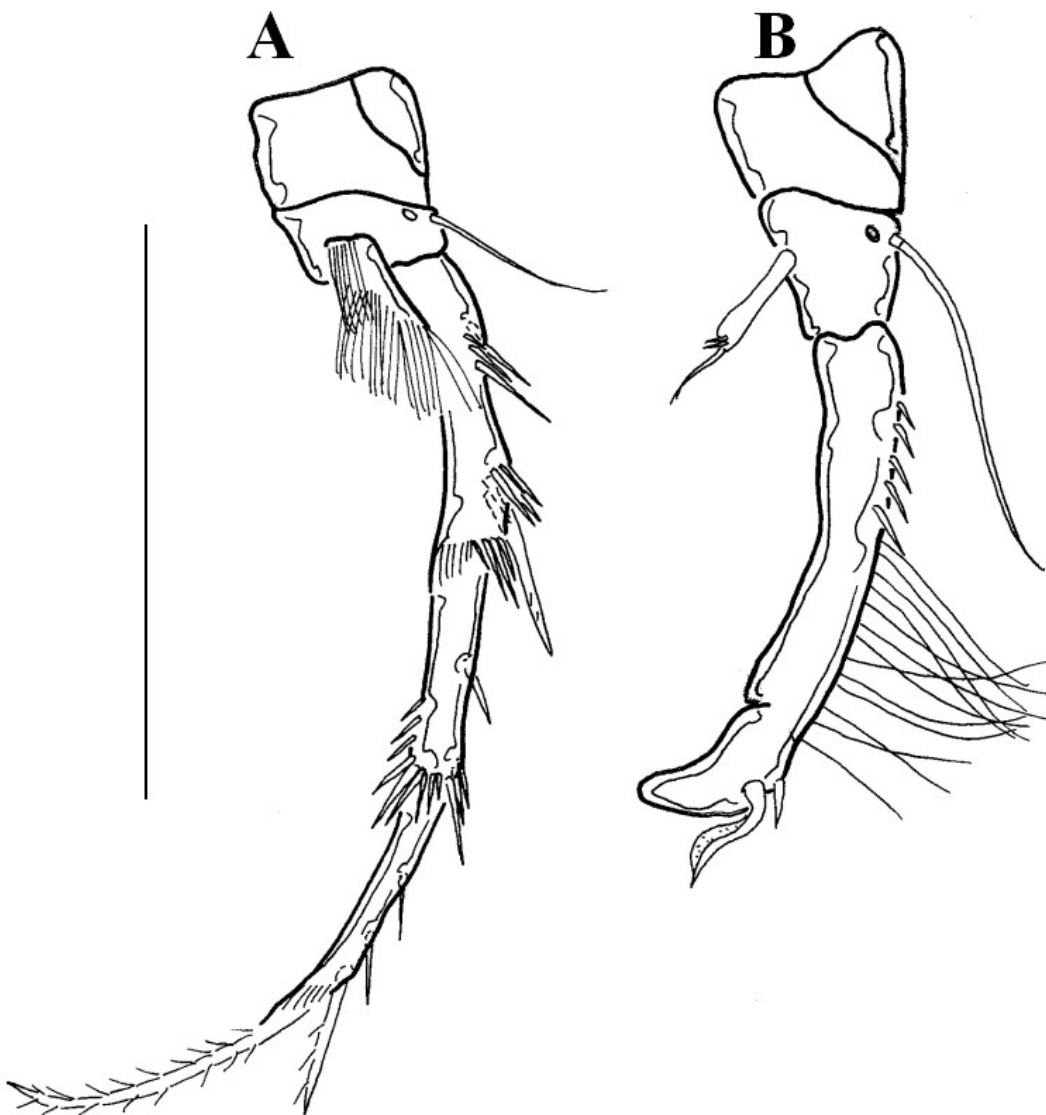


Figure 04- *Remaneicaris itacambirucui* n. sp., male. A, leg 4; B, leg 3. Scale bar= 50 μ m.

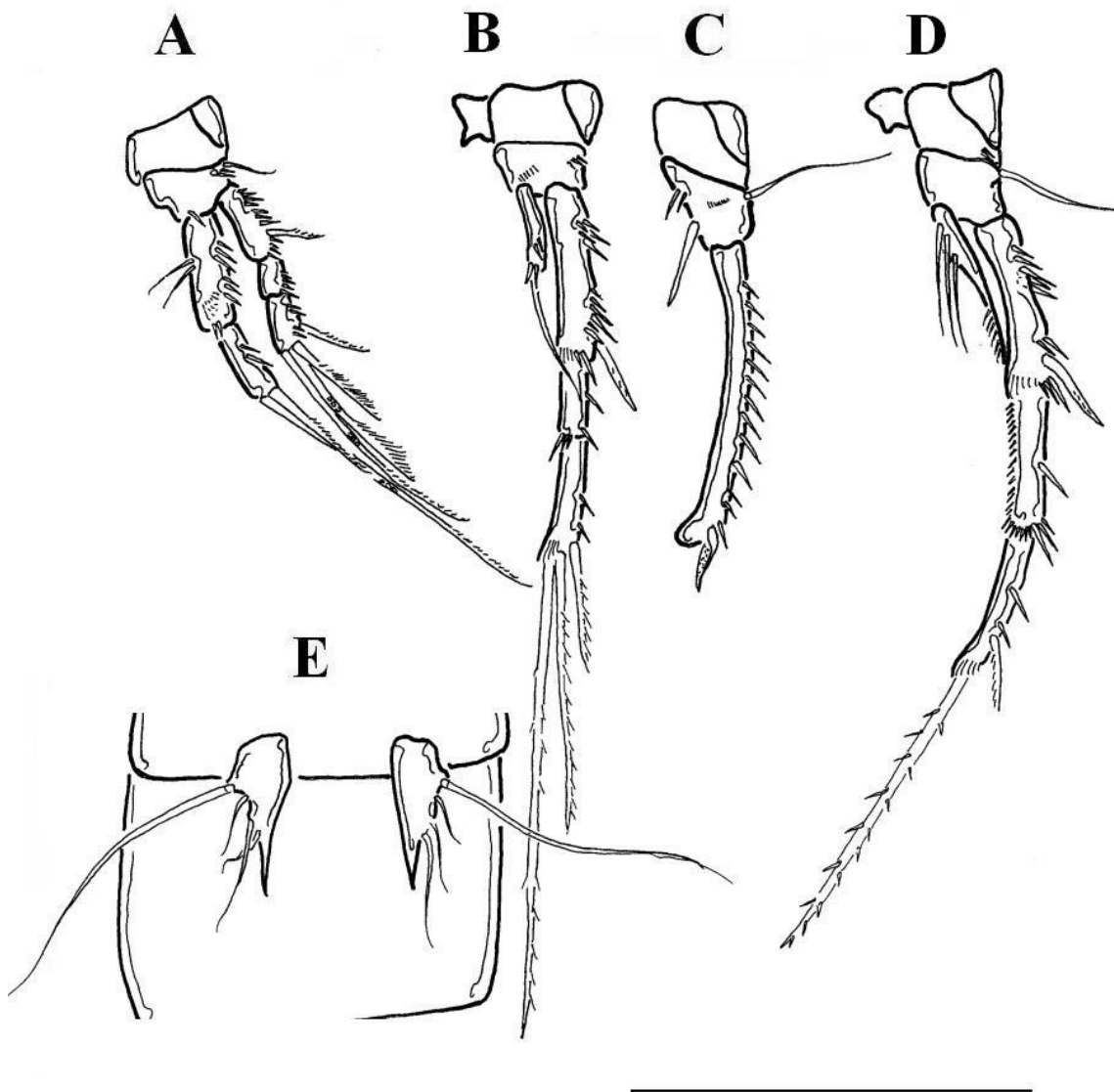


Figure 05- *Remaneicaris ivoneae* n. sp., male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar= 50 μ m.

Chapter V

The phylogenetic position of the genus *Remaneicaris* Jakobi (Copepoda, Harpacticoida, Parastenocarididae)

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Abstract

The genus *Remaneicaris* is monophyletic and its position within the family Parastenocarididae is tested using the method of cladistic systematics. The genus turned out to be basal within the family, being easily characterized by the subdistal position of the outer spine of leg 4 exp 3 as well as other very plesiomorphic characters, such as the presence of two setae on the first endite of Mx2. A new subfamily is proposed here to accommodate the genus *Remaneicaris*, sharing with it the same diagnosis. Finally, a diagnosis for each of the monophyletic groups within *Remaneicaris* is here given and the characters are discussed extensively. A key for the identification of the species within the genus is provided at the end.

Keywords: *Remaneicaris*, Remaneicaridinae, phylogeny, Neotropical, biogeography

1- Introduction

Copepoda Harpacticoida are small benthic Crustacea, usually smaller than 1.0 mm and operationally classified as meiofauna. Almost all families of Harpacticoida occur in marine

environments, from intertidal zones to abyssal environments (Lang 1948). Some of them, on sandy beaches, have invaded marine mesopsammic habitats (Higgins and Thiel 1988; Martínez Arbizu and Moura 1994). Only a few families have succeeded in colonising freshwater environments (Dussart and Defaye, 1990; Rouch, 1986). In this sense we can mention the families Phyllognathopodidae Gurney, 1932, Chappuisiidae Chappuis, 1949, Ameiridae Monard, 1927, Canthocamptidae Sars, 1906 and Parastenocarididae Chappuis, 1933.

The family Parastenocarididae is a monophyletic group and can be easily characterised and distinguished by the sexual dimorphism on the third pair of legs (as an apomorphy, the males have these appendices modified in a grasping organ, that allow the capture of the female during copulation (Glatzel, 1990)) and by the sexual dimorphism on the endopod of the leg 4. A more complete list of synapomorphies can be seen in Martínez and Moura (1994). With 241 species, they are typical interstitial groundwater inhabitants, being well adapted to life in the hyporheic zones of rivers as well as to life in continental aquifers. Their bodies are vermiform, and lengths very between 250 μm and 500 μm . They are completely transparent, without eyes and have very well developed nephridial and osmoregulatory organs, called integumental windows, on cephalotoracic and urosomal segments (Hosfeld and Schminke 1997).

Although composing a monophyletic group, the phylogenetical position of the parastenocaridids within Harpacticoida have been ground for some discussion in the past (viz. Kessler 1913; Schnitter and Chappuis 1914; Monard 1927; Pesta 1932; Chappuis 1933; Kunz 1938; Lang 1948; Martínez Arbizu and Moura 1994; Bruno *et al.* 1998) and within the family, different supraspecific groups (viz. Chappuis 1937; Kunz 1938; Lang 1948; Noodt 1962; Noodt 1963; Noodt 1972b), or genera (Jakobi 1969, 1972) have been created . Albeit weakly based on synapomorphies the Lang-Noodt system still is the best of what we have and most of the groups can be easily recognised and reworked toward monophyletic unities.

Nine genus have been proposed to accommodate the species of neotropical parastenocaridids (viz. *Parastenocaris* Kessler, 1913; *Remaneicaris* Jakobi, 1972; *Brasilibathynellocaris* Jakobi, 1972; *Forficatocaris* Jakobi, 1972; *Pararemaneicaris* Jakobi, 1972; *Siolicaris* Jakobi, 1972; *Paraforficatocaris* Jakobi, 1972; *Potamocaris* Dussart, 1979 and *Murunducaris* Reid, 1994); all of them occurring in Brazil.

With 28 species, *Remaneicaris* is the most diverse and widespread genus in South and Central America, being followed by *Forficatocaris* (13) and *Potamocaris* (6). Although being a well defined monophyletic group, even Noodt (1969) and later Jakobi (1972) distrusted the monophyletic condition of the group. In his work “Die Grundwasserfauna Südamerikas”, Noodt (1969) wrote: “Especially wide distributed (from Patagonia until Central America) we find the remaneicaris-group Noodt, with numerous species that, however, are obviously not homogeneous and need to be splitted in the future.” (“Besonderers weit verbreitet (Patagonien bis Zentral-Amerika) ist die remanei-gruppe Noodt mit bereits zahlreichen Arten, die jedoch offenbar noch inhomogen ist und weiterer Unterteilung bedarf”).

The objective of this study is to test the kinship within the genus *Remaneicaris*, as well as, between this genus within the family. Toward this objective here we give a list of characters, a data matrix (Table 1) and a diagram of the phylogenetic relationships within the genus *Remaneicaris* as well as between it and the family Parastenocarididae.

2- Methods

For the construction of kinship hypothesis the method of phylogenetic systematic of Hennig (1966) was used. For details see Hennig (1966), Ax (1984) and Wägele (2005). The cladogram (Fig. 1) was made by hand, using the Hennig principle (Meier 1992; Wägele 2005). Character states are here coded binary or multistate. Multistate characters were ordained. The condition for each

character can be seen in the character list. The data matrix is given in appendix 1. The polarisation of characters was done *a priori* by comparing the state of characters present in the ingroup (*Remaneicaris*) with the state of characters in other groups of Parastenocarididae, *Psammonitocrella* Rouch, 1992 and the families Ameiridae, Canthocamptidae and Leptopontiidae Lang, 1948 (*sensu* Martínez Arbizu and Moura 1994). Consequently, the final cladogram was rooted. The Hennig's criterion of parsimony (putative parsimony, Hennig 1966, Wägele 2004 and 2005) was adopted here. Additionally the computer program NONA (Goloboff 1999), supporting parsimony (cladistic parsimony), was employed in interface with WINCLADA (Nixon 1999). This program uses a heuristic algorithm with unconstrained search and multiple TBR+TBR as search strategy for the best topology and a Wagner algorithm that support character reversal (0-1 is equally possible as 1-0) as a “similarity” algorithm.

For the construction of the character matrix, the whole of Noodt's type material of Parastenocarididae, deposited at Deutscher Zentrum für Marine Biodiversitätsforschung (DZMB) from Senckenberg Forschungsinstitut und Naturmuseum in Wilhelmshaven (Germany), was observed. Additionally, some characters were extracted from literature as well as from direct observations of other parastenocaridids types and additional biological material deposited in the DZMB, University of Oldenburg (Germany), Muséum national d'Histoire naturelle (MNHM; Paris, France), Smithsonian Institut (Washington, USA), São Paulo University Museum (MUSP, Brazil) and Instituto Nacional de Pesquisas da Amazônia (INPA, Brazil).

The following taxa have been used for this study:

Outgroup- *Psammonitocrella* and Parastenocarididae (“Parastenocaridinae” and “Fontinalicaridinae” Schminke 1993, hereafter referred as Outgroup 1). The choice of the outgroups was based on a previous phylogeny proposed by Martínez Arbizu and Moura (1994). In accordance with these authors, the family Parastenocarididae is a sister taxon of the genus *Psammonitocrella*.

Ingroup- *Remaneicaris sensu* Corgosinho and Martínez Arbizu (2005) plus *R. tridactyla* n. sp., *R. paratridactyla* n. sp., *R. juliae* n. sp., *R. ivoneae* n. sp., *R. insolitus* n. sp. and *R. itacambirucui* n. sp. *Remaneicaris psammae* (Rouch, 1962) and *R. hexacantha* (Kiefer, 1936) were not included in the analysis, due to the lack of observable synapomorphies that could afford a better resolution of their position within the genus. However, their position within *Remaneicaris* is discussed in this work. *Parastenocaris ahaggarica* Bozic, 1978 was not included, due to some questionable characters present in the original description that were never found within the family Parastenocarididae. However its possible kinship with *Remaneicaris* is discussed here.

In this work there is no effort toward the resolution of the systematic position of the Parastenocarididae within the Harpacticoida. Therefore, following a previous hypothesis, the genus *Psammonitocrella* was adopted here as the sister group of Parastenocarididae (Martínez Arbizu and Moura 1994). For the construction of the computer derived phylogeny, the autapomorphies of a taxon formed by *Psammonitocrella* plus Parastenocarididae, as well as the autapomorphies of the family Parastenocarididae were critically adapted from the work of Martínez Arbizu and Moura (1994), being transcribed below with some amendments. There is no effort here toward the discussion of these characters.

Abbreviations used in the text are: A1= antennule, Mx2= maxilla, P1-P6= legs 1 to 6, exp= exopodite, enp= endopodite, (ap) = apomorphy, (pl) = plesiomorphy. The terms monophyletic, polyphyletic, paraphyletic, autoapomorphy, synapomorphy and plesiomorphy are used *sensu* Hennig (1966).

4- Results and Discussion

4.1- List of Characters

4.1.1- Synapomorphies for Parastenocaris plus *Psammonitocrella*

- A. Basis leg 2 with outer seta (0); without outer seta (1).
- B. Precoxal arthritis with two seta (0); with 1 surface seta (1).
- C. Enp 1 of leg 1 with inner seta (0); without inner seta (1).
- D. Enp 2 of leg 2 with two apical seta and one inner seta (0); with one apical seta (1).
- E. Enp 2 of leg 4 with two seta (0); with one apical seta (1).

4.1.2- Autapomorphies of *Psammonitocrella*

- F. Endopod leg 4: completely developed (0); reduced as a small protuberance (1).
- G. Mx2 syncoxa with two endites (0); with one endite (1).
- H. Mx1 coxa with 3 setae (0); with 2 setae (1).
- I. Basis leg 1 with outer seta (0); without outer seta (1) .

4.1.3- Autapomorphies of *Parastenocarididae*

- J. A2 endopod 2-segmented (0); divided in basis, allobasis and one endopod segment (1).
- K. Mandibular palp 2-segmented (0); 1-segmented (1).
- L. Leg 4 endopod without sexual dimorphism (0); with sexual dimorphism (1).
- M. Endopod leg1 3-segmented (0); 2-segmented (1).
- N. Leg 1 exopod 2 with inner seta (0); without inner seta (1).
- O. Exp 2 from leg 2 with outer seta (0); without outer seta (1).
- P. Exp 2 from leg 2 with inner seta (0); without inner seta (1).
- Q. Exp 2 from leg 3 with outer seta (0); without outer seta (1).
- R. Exp 2 from leg 3 with inner seta (0); without inner seta (1).
- S. Exp 2 from leg 4 with outer seta (0); without outer seta (1).
- T. Exp 2 from leg 4 with inner seta (0); without inner seta (1).
- U. Male leg 3 exopod is 3-segmented (0); transformed in a grasping organ (1).
- V. Female leg 3 endopod with free distal seta (0); distal seta incorporated to the segment (1).

³²This is an autoapomorphy also for *R. Ignotus*.

X. Integumental windows absent (0); present on cephalosome and urosomites 2-5 (1).

4.1.4- List of characters for *Remaneicaris* and less inclusive monophyletic groups

1. Male leg 3 endopod present (0); absent or reduced to one seta (1).
2. First Mx2 endite with two setae (0); with one setae (1).
3. Second Mx2 endite with three slender setae (0); with two slender setae and one seta transformed in a serrated spine like seta (1).
4. Basis leg 1 with inner seta (0); without inner seta (1).
5. Outer seta of leg 4 exp 3 in a distal position (0); in a subdistal position (1).
6. Leg 4 exp 3 with spinules displaced distally (0); with a spinule mesially displaced on the outer margin (1).
7. Leg 4 exp 2 with spinules displaced distally (0); with a spinule mesially displaced on the outer margin (1).
8. Leg 2 exp 3 with spinules displaced distally (0); with a spinule mesially displaced (1).
9. Leg 2 exp 2 with spinules displaced distally (0); with a spinule mesially displaced (1).
10. Leg 5 with intercoxal sclerite (0); without intercoxal sclerite (1).
11. Leg 1 enp 1 with an inner row of spinules (0); without this row of spinules (1).
12. Cuticle delicate, without any extra modification (0); cuticle very chitinized and perforated (1).
13. Proximal zone of exp 1 of leg 4 with an external row of spinules distributed in line (0); distributed in a discrete “v” line (1); distributed in an accentuated “V” line (2).
14. Integumental windows: dorsal on urosomites 2 until 5 (0); lost on urosomites 3 and 4 (1); Lateral on urosomite 5 and dorsal on urosomite 2 (2); lateral on urosomite 2 and 5 (3).
15. Leg 5 in a more ventral position (0); displaced in a more ventro-lateral position (1).

16. Leg 5 without inner process, setae distally arranged (0); with an inner process, setae shifted to the outer margin (1).
17. Male leg 3, apophysis: chitinous (0); with an inwardly turned hyaline margin forming 90° with the main axis of the exp of leg 3 (1).
18. Male leg 3, exp 1, distal spinule (spinule anterior to the insertion of the outer spine (thumb)): unmodified (0); modified (1).
19. Male leg 3, exp 2: Without any specialization (0); with a quitinous plate anterior to the apophysis.
20. Furca, inner margin: unmodified (0); concave (1).
21. Male leg 3, exp 1, distal spinule: without hyaline margin (0); with a hyaline margin (1).
22. Endopod leg 3, male: Smaller than 2/3 of the exopod (0); bigger than 2/3 of the exopod (1).
23. Leg 4 exp 2 without ornamentation on the inner margin (0); with a longitudinal row of spinules (1).
24. Males A1, last segment, without any transformation (0); with a hyaline edge (1).
25. Telson: paraopercular area without spinules (0); with spinules (1); ornamentation not formed or lost (2).
26. Telson: ventral side smooth (0); with a linear row of spinules (1).
27. Leg 3, male: endopod thin and straight (0); oval (1).
28. Leg 2, male: endopod is short, not reaching the level of insertion of the outer spine of the exp 1 (0); endopod is long, reaching the level of insertion of the outer spine of the exp 1.
29. Leg 4 endopod, female: smaller than exp 1 (0); bigger than exp 1 (1).
30. Telson, ventral side: small spinules near the insertion of the furca (0); two or more big spinules near the insertion of the furca (1).

31. Furca without ornamentation (0); with 2-3 dorsal and subdistal spinules (1); without this character (2).
32. Thumb without hyaline margin (0); with a hyaline margin (1)
33. Leg 3, male: exp inner margin without ornamentation (0); inner margin with spinules on the proximal region (1).
34. Male leg three: presence of an endopod (0); non formation of the endopod (represented by a single seta) (1).
35. Male leg 4: basis without ornamentation on the inner margin (0); basis with an inner row of strong spinules (1).
36. Male leg 4: basis without spinules near the insertion of the endopod (0); with a row of long spinules near the insertion of the endopod (1); ornamentation reduced to a row of small spinules near the insertion of the endopod (2).
37. Male leg 4: basis well cuticularized near the insertion of the endopod (0); low cuticularized near the insertion of the endopod (1); recuticularization of this area (non formation of the cuticularized area) (2).
38. Male A1: last segment with a modified seta (1); without this character (0).
39. Leg 3: thumb is a normal spine (0); thumb is a triphid spine (1).
40. Female, fifth urosomite: smooth (0); with dorsal ornamentation (1).
41. Male, fifth urosomite: smooth (0); with dorsal ornamentation (1).
42. Leg 6, female: reduced to unarmed plates over the genital aperture (0); plates armed with two setae each (1); non formation of armature (2).
43. Leg 3, male: straight and without any expanded region (0); inner proximal region is expanded (1).
44. Telson: without dorsal ornamentation (0); with a row of spinules prior to the operculum (1).

45. Leg 3, male: inner margin of basis without ornamentation (0); inner margin with long spinules (1).
46. Leg 4, female: inner margin of basis without ornamentation (0); inner margin with a row of long spinules (1).
47. Leg 3, male: apophysis with rounded distal rim and longer than broad (1); without this combination of characters (0).
48. Leg 3, male: apophysis inward curved in less than 90° (0); inward curved in 90° (1); inward curved in more than 90° (2).
49. Leg 4, female: blade shaped (1); without this character (0).
50. Leg 3, male: without distal depression (0); with a distal depression (1).

4.2- Monophyly of *Remaneicaris* and the subfamily Remaneicaridinae subfam. nov.

Here I propose that *Remaneicaris* is the most basal genus within the family, being the sister group of all other Parastenocarididae and constituting a new subfamily within it. The diagnose for the new subfamily is the same proposed by Corgosinho and Martínez Arbizu (2005) for the genus:

Family Parastenocarididae

Subfamily Remaneicaridinae subfam. nov.

Diagnosis: Parastenocarididae with 9-segmented antennule in male (pl) and 7-segmented antennule in female (pl). Male antennule haplocer (pl). Mx2 with 2 endites, proximal endite with 2 seta (pl); distal endite with three slender setae (pl). P1 endopod nor sexually dimorphic (pl). P2 and P4 middle and distal exopodal segments with long spinule located mesially on outer margin (ap). P4 distal exopodal segment with distal outer seta shifted to subdistal position (ap). Male P3 with endopodal segment bearing one seta (pl), apophysis rounded without setae (pl). Male P4 enp leaf-

shaped and hirsute. P5 without sexual dimorphism (pl), displaced to ventro-lateral position (ap) and lacking intercoxal sclerite (ap). Furca with all three anterolateral setae located on distal third.

Despite the high diversity in ground waters and the relatively high number of described species, there are only few agreements about the “validity” or “monophyletic status” of some genera and supraspecific groups within the family Parastenocarididae. Chappuis (1937), following the Germanic tradition, tried to separate the different species of *Parastenocaris* Kessler, 1913 in four different groups based on the morphology of the basis and endopod of the male P4. Later, Lang (1948) revised Chappuis’ (1937) system and proposed the groups *brevipes*, *minuta*, *nana*, *cujensis*, *musciicola*, *fontinalis*, *staheli*, an adopted also the group *proserpina* (Kunz, 1938), proposed earlier. Noodt (1962,1963, 1972b) added five more groups to Lang’s system, *panamericana* (Noodt, 1962), *forficata* (Noodt, 1963), *sioli* (Noodt, 1963), *remanei* (Noodt, 1963) and *columbiensis* (Noodt, 1972).

Most of these groups were reworked by Jakobi (1972) raising some of them to the genus level, creating some new ones. Interestingly most of Jakobi’s genera were not accepted by other authors (i.e. Rouch 1986; Dussart and Defaye 1990; Ahnert 1994; Reid 1994; Reid 1998 and Galassi and De Laurentiis 2004) and their artificial construction were correctly criticized by Schminke (1976). However, *Forficatocaris* and *Paraforficatocaris* (junior synonym of *Brasilibathynellocaris* Jakobi, 1972 (Corgosinho and Martínez Arbizu in prep.)) were fully adopted and, paradoxically, remained almost as a consensus the use of Lang’s (1948) and Noodt’s (1962, 1963, 1972b) “systems” in posterior works. Later Schminke (1993; pers. comm.) correctly accepted the genus *Cafferocaris* Jakobi, 1972 as being monophyletic after short amendment. Other genera (viz. *Potamocaris* Dussart, 1979; *Murunducaris* Reid, 1994 and *Simplicaris* Galassi and De Laurentiis, 2004), however, continued to be created and accepted without, or with a superficial phylogenetical reasoning.

In my opinion, the confusion about the validity of the genera is mainly due to the misinterpretation of the ICZN (viz. ICZN 2002) and also, due the confusion between “validity” and the phylogenetic condition of the genus. In other words it is a dogma that on the light of a phylogenetical reasoning a genus, to be valid, need to be natural (monophyletic). However, the simple creation of a genus based only in the assumption of monophyly is not good enough in a phylogenetical context. In fact, with this practice we only assure that the species belonging to a given genus have a common ancestor, but without a broad overview of other groups, we risk to force a paraphyletic group adjacent to it. Aiming the resolution of these problems, first we should revalidate all those genera that are in accordance with the rules of validity of the ICZN and thus, within a broad phylogenetic context, we can proceed toward its revalidation or extinction.

Considering this, recently Corgosinho and Martínez Arbizu (2005) deeply rearranged the genus *Remaneicaris*, removing *P. staheli* (Menzel, 1916), *P. itica* (Noodt, 1962) and *P. dactyloides* (Kiefer, 1967), previously placed in the genus by Jakobi (1972) and included *R. membranacea* (Noodt, 1965) and *R. ignotus* (Dussart, 1983) on it. Additionally they provided a new diagnosis based also on synapomorphies and favoured the revalidation of the genus.

The result of the computer derived phylogenetical analysis was one most parsimonious tree with 114 steps in length (CI= 0.76; RI= 0.88), with exactly the same topology and character distribution obtained after the manual argumentation. The high RI and CI values express here the relatively high amount of putative synapomorphies and the low number of homoplasies respectively. However, as pointed out by Wägele (2005), these cladistic statistics do not say anything about the quality of the data, or about the probability of evolution of characters or of groups of species.

From a total of 72 characters, 48 in the ingroup, only 12 are homoplastic, being them characters I, 14, 17, 20, 25, 29, 30, 32, 36, 37, 44, 46 and 48. Only character 25 is a synapomorphy

in more than one level; the others occur as synapomorphies in one single level and also as an autoapomorphy for single species. Characters 32 and 37 are the most variable, with five steps each.

The sister group of *Remaneicaris*, a taxon formed by the subfamilies “Parastenocaridinae” and “Fontinalicaridinae” (outgroup 1) can be well defined by the absence of an endopod in male leg 3 (char. 1, fig. 2), the presence of one setae on the proximal endite of Mx2 (char. 2)), the presence of three elements on the distal endite of Mx2 (one of these elements transformed in a serrated spine (char. 3) and by the loss of an inner seta on the basis of leg 1 (char. 4). Even considering the absence of the inner basal setae of leg 1 on the groundpattern of the family, appearing independently in different species within Parastenocarididae, here is worth of mention that the identical modification suffered by the setae of the 1st and 2nd endites of Mx2 (lost of one seta on the first endite and the transformation of one seta into a serrated spine on the second endite) is a good support for the phylogenetic hypothesis proposed here. The alternative, with the inclusion of *Remaneicaris* within the “Parastenocaridinae” would imply the appearance of such modifications mentioned above at least two times.

Within the family Parastenocarididae, only *Remaneicaris* species retained an endopod on the leg 3 of males (Fig. 2 B). This structure have been described and/or figured by Jakobi (1962), Noodt (1963, 1965, 1972a), Kiefer (1967) and Dussart (1983) and its presence was confirmed in this work. Only a few derived species within this genus (viz. *R. euniceae* Corgosinho and Martínez Arbizu, 2005; *R. analuizae* Corgosinho and Martínez Arbizu, 2005 and *R. oncophora* (Noodt, 1965)) have the enp reduced to a seta, due to the non formation of the ramus. In accordance with Schminke (pers. comm.), the condition that can be seen in other species within *Remaneicaris* such *R. ciliata*, *R. sanctiludovici*, *R. drepanephora*, *R. palaciosi*, etc, could be in fact not an unisegmented enp, but a transformed spine. Even considering that the enp is modified into a transformed seta in other species within *Remaneicaris*, it is still more parsimonious to consider an unisegmented enp on the

groundpattern of the genus. Its of this structure is a plesiomorphic character and reinforces the basal position of the genus *Remaneicaris*. The remaining parastenocaridids share the withered endopod of male leg 3 as a synapomorphy. The description of this structure, in other parastenocaridids, such as the species belonging to Noodt's *panamericana*-group (Noodt, 1962), is erroneous and the observation of the original material revealed that the endopod described by Noodt (1962) as “stiftförmiger Enp.” is, in fact, a transformed spinule, being the true endopod represented by a reduced seta (Fig. 2 A).

Remaneicaris share, as a symplesiomorphy, the presence of two setae on the proximal Mx2 endite. The presence of this structure in other species has been discussed by Corgosinho and Martínez Arbizu (2005) and Corgosinho *et al* (2007). These authors concluded that within the Parastenocarididae, only *Remaneicaris* hold this character and that the pattern present in *P. ahaggarica* Bozic, 1978 deserves re-confirmation.

An alternative argumentation would be to interpret *Remaneicaris* as a monophyletic group within the “Parastenocaridinae” (Schminke pers. comm.). However, this assumption would imply additional steps that should be explained by reversion of characters within *Remaneicaris* or as convergence between “Parastenocaridinae” and “Fontinalicaridinae”. In my view reversions can be a common event in evolution and could be well explained by the expression of a homeotic gene via the suppression of a gene repressor. In accordance with Ferrari (1988), this would be the mechanism involved in copepod legs development. But here, if we accept *Remaneicaris* as a “Parastenocaridinae”, some clear plesiomorphies of the genus, such as the presence of endopod on male leg 3 and the already mentioned armature on Mx2, should be interpreted as autapomorphies (reversion), or maintained as a plesiomorphy, thus, being lost at least two times within the family. Therefore, on view of the facts, I choose the most parsimonious hypothesis.

The loss of the inner seta on the basis of leg 1 is a character that evolved within *Remaneicaris*, being a synapomorphy for a taxon formed by *R. meyerabichi* (Noodt, 1962) plus all other *Remaneicaris*, viz. (*R. meyerabichi* (*Remaneicaris* spp.)). Inner setae is a character present in the groundpattern of the family (Corgosinho *et al.*, *in press.*) and also occurs in the groundpattern of the genus, being expressed in *R. ignotus*. According to Martínez Arbizu and Moura (1994), the family Parastenocarididae shares the loss of the inner seta on the basis of leg 1 as an autapomorphy. However, the presence of this structure in the most basal genus of the family and specially in *R. ignotus*, the most basal species within the genus, suggests that it should be interpreted as a symplesiomorphy of Parastenocarididae.

The monophyletic status of *Remaneicaris* is based on the characters 05 - 10. Character 5 (Fig. 2 C; the subdistal position of the outer seta on the exp 3 of leg 4) constitute what Corgosinho and Martínez Arbizu (2005) consider the most important synapomorphy of *Remaneicaris*. In accordance with these authors, the homologous seta is displaced also in other species, such as in *Parastenocaris spinosa* Wells, 1964, *P. spinipes* Wells, 1964 from Africa and *P. pusillus* Chappuis, 1954 and *P. trisaetosa* Chappuis, 1954 from Madagascar. However this have been interpreted as the result of convergent evolution on the light of reciprocal illumination provided by the type of modification and clasping behaviour of the male antennule (Corgosinho and Martínez Arbizu 2005). In accordance with these authors, the geniculation mode of the male antennule in *P. spinosa*, *P. spinipes*, *P. pusillus* and *P. trisaetosa* belongs to a special type where the 8th (penultimate) segment is transformed, displaying a strong process on the inner distal margin. So, the difference is, when in *Remaneicaris* the the 8th segment move against the 7th segment and the 9th (distal) segment bents dorsally over the 5th segment, in the African species, the 9th segment is moved outwardly and has no function in clasping. According to Schminke (1993, and pers. comm.) this type of antennule is an autapomorphy of the “Parastenocaridinae”. Since *Remaneicaris* do not

belong to the crown-group “Parastenocaridinae” (Corgosinho and Martínez Arbizu 2005), therefore cannot be related to the species from Africa and Madagascar. *Parastenocaris ahaggarica*, from Africa, also have the outer spine from leg 4 exp 3 shifted to a subdistal position and shares with *Remaneicaris* some other interesting characters. However, the Mx1 structure is quite unusual, even considering the whole family. Hence, it is not included here in the phylogenetical analysis, being considered as *Remaneicaris incerta sedis*.

Another autapomorphy of *Remaneicaris* is the presence of a long and medial spinule on the outer margins of exp 2 and 3 of legs 2 and 4 (chars. 6 -9). These characters seem to appear only in some African *Parastenocaris*, viz. *P. quollensis* Cottarelli and Bruno, 1995, *P. aethiopica* Cottarelli and Bruno, 1995, *P. cataractae* Cottarelli, 1982, *P. sinoiaica* Wells, 1964, *P. fluviatilis* Wells, 1964 and *P. cornuta* Chappuis, 1955, but the illustrations are not detailed enough to allow a positive identification of such structures. If confirmed the presence of similar ornamentation on these African species, this should not be considered a synapomorphies for both groups.

Another important character in this phylogeny concerns the absence of the intercoxal sclerite of the leg 5 on members of *Remaneicaris*. It is difficult to know if other parastenocaridids also have lost the intercoxal sclerite, because this character is seldom described. Thus, here I consider the lack of the intercoxal sclerite of leg 5 as an autapomorphy for *Remaneicaris* (char. 10). With the exception of the genus *Simplicaris* Galassi and de Laurentiis, 2004, that have lost the entire leg 5 and two other species placed on it as *incerta sedis* (viz. *P. hippuris* Hertzog, 1938 and *P. aedes* Hertzog, 1938), it seems that a leg 5 connected by an intercoxal plate is present at the ground pattern of all Parastenocarididae.

4.3- Phylogenetic position and diagnosis of the monophyletic groups within *Remaneicaris*

The morphological study of the genus revealed the possible existence of some monophyletic groups that were later tested and supported by the phylogenetical analysis.

In accordance with Schminke (pers. comm.), the genus *Remaneicaris* is composed by some very different organisms from different evolutionary trends and that should be splitted in different genera. This idea also echoes in the past. For example, the monophyletic condition of the group was distrusted by Noodt (1965 and 1969) in view of the diversity of different morphological tendencies observed in groups from different geographical areas within South America. In accordance with this author (Noodt 1965), the *remanei*-group would be formed by “*inhomogen*” unities that should be splitted in the future.

The separation of species and groups of species in new genera or subgeneric monophyletic groups is not a simple task in taxonomy and the criteria adopted are very diverse and controversial. For example, some authors prefer to create new genera in view of some novelties, however, without question the true synapomorphic condition of the character or even, the strength of it (if it is too homoplastic or not). Furthermore, new monophyletic genera have been erected based only in the assumption of monophyly of the group, without the consideration of its position within a bigger group. Thus, even being well founded in autoapomorphies, the rising of a group to a generic status can have, as a consequence, the concomitant creation of a paraphyletic taxon as already mentioned above.

Here we do not face any of these problems. In fact, it would be fair reasonable the creation of different monophyletic genera within *Remaneicaris*. I agree almost completely with Schminke's ideas. However, the splitting of the genus in smaller ones would imply the “weakening” of the diagnosis of each monophylum, making sometimes difficult, for other researches, to well identify the groups, since some of the characters used to define the monophyletic groups within *Remaneicaris* are difficult to see without a good optical resolution. Hence, we have opted to

maintain the genus *Remaneicaris* to all the species grouped around *R. remanei* (Noodt, 1963) *sensu* Corgosinho and Martínez Arbizu (2005).

Another problem involved concerns the identification of the females, since its separation from other species and the discernment of to which group do they belong depend, in most cases, of the presence of the males in the sample.

Besides, this is the first hypothesis about the phylogeny of *Remaneicaris* and albeit most of the groups seem to be very well supported by good autapomorphies, this scenario can change with the observation of new material, what could make soundless the adoption of a new genus here. Therefore, here I have opted for the most conservative approach, simply naming what I believe to be good monophyletic groups within the genus, as follows:

***argentina* - group nov.**

Diagnosis: *Remaneicaris*. Telson smooth (pl). Last segment of male antennule without modified seta (pl) or hyaline margin (pl). Leg 1 endopod not sexually dimorphic (pl) and without ornamentation on the inner margin (ap). Leg 3 with a hyaline margin in apophysis (ap); a modified distal spinule on the outer margin of leg 3 (ap). Basis of male leg 4 without ornamentation (pl); exp1 with a proximal row of spinules arranged in a soft “v” on the outer margin (pl); exp 2 without ornamentation on the inner margin (pl). Leg 5 displaced to a ventro-lateral position (pl) and with small inner process, with the setae distally arranged (pl). List of species: *R. argentina* (Noodt, 1965), *R. jujuyensis* (Noodt, 1965), *R. drepanephora* (Kiefer, 1967), *R. palaciosi* (Noodt, 1962), *R. clandestina* (Noodt, 1963) and *R. hurdi* (Jakobi and Silva, 1962). Species *incerta sedis*: *P. ahaggarica* and *R. psammae* (Rouch, 1962).

***analuizae* - group nov.**

Diagnosis: *Remaneicaris*. Telson with (ap) or without spinules on the paraopercular region. Male last segment of antennule with a distal hyaline margin (ap). Leg 1 endopod not sexually dimorphic (pl) and with a row of spinules on the inner margin (pl). Leg 3 of males straight, outer margin generally ornamented (pl?) and without a hyaline apophysis (pl); with (pl) or without endopod (ap; viz *R. analuizae* and *R. euniceae*). Basis of male leg 4 without ornamentation (pl); exp1 with a proximal row of spinules arranged in a well developed “V” on the outer margin (pl); exp 2 with a row of spinules on the inner margin (pl). Leg 5 displaced to a ventro-lateral position (pl) and with well developed inner process, with setae outwardly displaced (pl). List of species: *R. itacambirucui* n. sp., *R. ivoneae* n. sp., *R. insolitus* n. sp., *R. divae* (Noodt, 1972), *R. tageae* (Noodt, 1972), *R. analuizae* and *R. euniceae*.

***tridactyla* - group nov.**

Diagnosis: *Remaneicaris*. Telson with spinules on the region prior to the operculum, before the insertion of the sensilla (ap); ventrally with two or more big spinules near the insertion of the furca. Last segment of male antennule with a modified seta on the last segment (pl). Leg 1 endopod not sexually dimorphic (pl) and with a row of spinules on the inner margin (pl). Basis of male leg 4 with an inner row of strong spinules (pl); a well developed row of spinules near the insertion of the endopod (pl), rising from a low cuticularized margin (pl); exp1 with a proximal row of spinules arranged in a well developed “V” on the outer margin (pl); exp 2 with a row of spinules on the inner margin (pl). Leg 5 displaced to a ventro-lateral position (pl) and with well developed inner process, with setae outwardly displaced (pl). List of species : *R. tridactyla* n. sp., *R. paratrindactyla* n. sp., *R. paraensis* (Noodt, 1963), *R. juliae* n. sp., *R. paraguayensis* (Noodt, 1963) and *R. remanei* (Noodt, 1963). Species *incertae sedis*: *R. hexacantha* (Kiefer, 1936).

***cordobaensis* - group nov.**

Diagnosis: *Remaneicaris*. Telson smooth (pl). Last segment of male antennule with a modified seta on the last segment (pl). Leg 1 endopod not sexually dimorphic (pl) and with a row of spinules on the inner margin (pl). Male, leg 3 is proximally dilated (ap) and with apophysis inwardly curved in 90° (ap). Basis of male leg 4 with an inner row of strong spinules (pl); with (viz. *R. sanctiludovici* (Noodt, 1965); pl) or without (ap) a well developed row of spinules near the insertion of the endopod (pl); with (viz. *R. sanctiludovici*; pl) or without (ap) a low cuticularized margin near the endopod insertion; exp1 with a proximal row of spinules arranged in a well developed “V” on the outer margin (pl); exp 2 with a row of spinules on the inner margin (pl). Leg 5 displaced to a ventro-lateral position (pl) and with well developed inner process, with setae outwardly arranged (pl). Leg 6 armed with two spines or seta (pl). List of species: *R. ciliata* (Noodt, 1965), *R. cordobaensis* (Noodt, 1965), *R. sierrae* (Noodt, 1965) and *R. sanctiludovici*.

***persephone* - group nov.**

Diagnosis: *Remaneicaris*. Telson smooth (pl); integumental window in the second urosomite is divided in two dorsolateral windows (ap). Last segment of male antennule with a modified seta on the last segment (pl). Leg 1 endopod not sexually dimorphic (pl) and with a row of spinules on the inner margin (pl). Basis of male leg 4 with an inner row of strong spinules (pl); with (pl) or without (viz. *R. rhizophora* (Noodt, 1965); ap) a well developed row of spinules near the insertion of the endopod (pl); with (pl) or without (viz. *R. membranacea* (Noodt, 1965) and *R. rhizophora*; ap) a poorly cuticularized margin near the endopod insertion; exp1 with a proximal row of spinules arranged in a well developed “V” on the outer margin (pl); exp 2 with a row of spinules on the inner margin (pl). Leg 5 displaced to a ventro-lateral position (pl) and with well developed inner process,

with setae outwardly displaced (pl). With (pl) or without (viz. *R. membranacea* and *R. rhizophora*; ap) leg 6 armed with two spines or seta (pl). List of species: *R. hecate* (Noodt, 1965); *R. oncophora* (Noodt, 1965); *R. persephone* (Noodt, 1965); *R. pluto* (Noodt, 1965); *R. membranacea* and *R. rhizophora*.

Within *Remaneicaris*, *R. ignotus* is the sister group of all remaining species (hereafter named ingroup 2). For redescription of *R. ignotus* and discussion of characters see Corgosinho *et al.* (*in press.*). The ingroup 2 can be well defined by the characters 4, 13 (st. 1), 14 (st. 1), 15 and 16. Although not present in all members inside this ingroup, the presence of characters 13 (st. 1) and 14 (st. 1) as synapomorphies is based on the deduction of the groundpattern at this level by the application of the outgroup comparison and/or the application of the Hennigian “criterion of correlation of series of transformation” (CCST); thus, permitting the creation of hypothetical series of transformation for multistate characters.

The migration of the leg 5 to a more ventro-lateral position (char. 15), in opposition to the more ventral position found in *R. ignotus*, is one of the most clear synapomorphies at this level. Concerning the morphology of the leg 5, within *Remaneicaris*, the most plesiomorphic condition of this limb can be seen in *R. ignotus* (Fig 3 A). In this species, there is not an inner cuticular process in male leg 5, and the three exp setae are located in a distal position, conferring a square configuration to this limb. Only in the females we can see a small inner cuticular process. However, it occurs in a lower level than the setae and the distal position of the armature is maintained (plesiomorphy). All other species of *Remaneicaris* have a more (Fig. 3 C) or less developed (Fig. 3 B) inner process in leg 5, that culminate with the lateral placement of leg 5 armature (char. 16). In other species this process has secondarily disappeared, conferring a bilobed shape to the leg (viz. *R. analuizae* e *R. paraensis*) (Fig 3 D).

Character 14 is one of the most striking series of transformation within *Remaneicaris* and can be used to define different monophyletic groups at different levels of generality. In accordance with Corgosinho and Martínez Arbizu (2005), the presence of dorsal integumental windows on cephalotorax and in all urosomites seems to be a character present in the ground-pattern of Parastenocarididae. In a recent paper these authors proposed a series of transformation for this character. However, this scenario showed to be not in accordance with the phylogeny at hand. Thus, in *R. ignotus* all the urosomites have one dorsal integumental window, a plesiomorphic condition shared with the outgroup 1. In *R. meyerabichi* (Noodt, 1962) and *R. palaciosi* a dorsal integumental window occurs in the 2nd and 5th urosomites. This character state in *R. palaciosi* is definitely a reversion to the state present at the basis, after the separation between *R. ignotus* and the ingroup 2. So, after the branching point between *R. ignotus* and the ingroup 2, marked by the loss of the dorsal integumental windows on urosomites 3 and 4 and its permanence in the 5th urosomite, the next step is represented by the splitting of the 5th urosomite into lateral windows as a synapomorphy for the remaining *Remaneicaris* (hereafter named ingroup 3), except of *R. meyerabichi*. Although not supported by the actual data, more samples taken in other regions can give different information that could support the intermediate stages proposed by Corgosinho and Martínez Arbizu (2005).

Character 13 (viz. exp1 of leg 4 with a proximal row of spinules arranged in a soft “v” on the outer margin) is a very diagnostic plesiomorphy for the *argentina*-group nov. The remaining species (ingroup 4) share as a synapomorphy the presence of a well developed “V” row of spinules on this segment. Outside *Remaneicaris*, no Parastenocarididae have a proximal row of spinules arranged in “v” on the proximal margin of leg 4 exp 1. In *R. ignotus* and in the species that compose the outgroup 1, to our knowledge, the proximal row of spinules on the outer margin of leg 4 exp 1 is linearly arranged.

The most important autapomorphies of the *argentina*-group nov. are the presence of an apophysis with a hyaline margin (char. 17) and of a modified spinule on the distal margin of the exp 1 of male leg 3, juxtaposed to the thumb insertion (char. 18). Within *Remaneicaris* only *R. paraguayensis* and *R. divae* also have a hyaline apophysis on leg 3. However, these species belong to different monophyletic groups within ingroup 4, namely *tridactyla* group nov. and *analuizae* group nov. A closer observation of these characters revealed that in *R. divae*, the apophysis is a hyaline bud at the distal rim of a straight leg 3 and the thumb is a very long and straight spine, without the adjacent modified spinule. In *R. paraguayensis* the hyaline margin surround the whole rounded apophysis and a modified spinule at the distal rim of exp 1 of leg 3 is also absent. In the *argentina*-group nov., on the contrary, the apophysis have a very characteristic shape, with a well developed hyaline margin, inwardly turned (commonly with a “pointed” edge), at the end of a straight exopod, conferring to it a final angle of approximately 90° with the main exopod axis. Besides, ingroup 4 do not share the presence of a hyaline apophysis in the groundpattern. Thus, the presence of this character within *Remaneicaris*, outside the *argentina*-group nov., should be seen as a homoplasy. Within the Parastenocarididae, other species and groups also have an apophysis with a hyaline margin. We can mention *P. arenosus* Fryer, 1956, *P. monodi* Chappuis, 1959, *P. marlieri* Chappuis, 1955, *P. crassicaudis* Chappuis, 1955, *P. tapajoensis* Noodt, 1963, most of *Forficatocaris* species, the *panamericana*-group nov. and some *Potamocaris*. However, these species belong to different evolutionary lines within the Parastenocarididae and thus, the presence of this structure is not homologous.

Another very distinctive autapomorphy of the *argentina*-group nov. is the absence of an inner row of spinules on the inner margin of enp 1 of leg 1 (char. 11). All other *Remaneicaris* of the ingroup 4 (viz. *analuizae*, *tridactyla*, *persephone* and *cordobaensis* group nov.) have retained this row of spinules. Lang (1948) had already mentioned the importance of this structure, although

referring to it as an “innere Borste” (inner seta). In fact, no Parastenocarididae have an inner seta on the endopod 1 of leg 1. In accordance with Martínez Arbizu and Moura (1994), the loss of this seta is one of the most important synapomorphies of a taxon formed by *Psammonitocrella* + Parastenocarididae. However, the presence of an inner ornamentation on the enp of leg 1 is widespread in different evolutionary lineages and have been used to define monophyletic groups within Parastenocarididae (i.e. Ahnert 1994 used the presence of inner modified spinules on the enp 1 of leg 1 for the definition of *Potamocaris/Forficatocaris*). Besides, it is also present in *Psammonitocrella* and probably it is present in the groundpattern of a bigger group around Parastenocarididae.

Besides character 13 (st. 2), the ingroup 4 is well defined by the presence of an inner row of spinules on exp 2 of leg 4 (char. 23). The same structure appears in other species outside *Remaneicaris*, but in these cases, it seems restricted to some unrelated species within “Fontinalicaridinae”.

Within ingroup 4, the *analuzae*-group nov. is characterized by the presence of a hyaline margin on male A1. This is a unique character within *Remaneicaris* and do not appear even in other parastenocaridids. This character has never been observed in *R. tageae* and *R. divae*. However, the presence of paraopercular ornamentation on these species along with the morphology of the leg 3 of males, with a continuous row of spinules on the outer margin, the shape of leg 4 endopod also in males and the presence of less conspicuous characters such as the inner spinules on the proximal region of male leg 3 (char. 33), the presence of 2-3 dorsal spinules on the medial region of the furca (char. 31) and the absence of other structures only observed in other monophyletic groups, suggest the identity of these species as members of the *analuzae*-group nov. In this case, the absence of a hyaline margin in male A1 of *R. divae* and *R. tageae*, if observed, need to be considered as an independent reversion.

Moving “upward” in the phylogeny, the next step is a taxon formed by the *tridactyla*, *cordobaensis* and *persephone* group nov., plus *R. icoaraci* as an *incerta sedis* species (ingroup 5). Ingroup 5 share some very unusual modifications on the basis of male leg 4 (Char. 35-37), as well as a modified seta on the last segment of male A1 (char. 38).

An inner row of spinules on the inner margin of the basis of the leg 4 of males is present in all members of ingroup 5 and it seems to have been figured, outside *Remaneicaris*, at least for *P. delamarei* Chappuis (1958), as making part of the “endopod”. Normally the fine ornamentation was omitted in old descriptions, making difficult to say if this structure is present in other groups within the family or not. For example, a closer observation of an apparently homologous structure present in *Brasilibathynellocaris* spp revealed a strong difference in form and position. Hence, the two strong “spines” present proximally on the inner margin of the “basis” of male leg 4 of *Brasilibathynellocaris* spp. (viz diagnose for the *panamericana*-group nov. in Noodt 1962, pg 246) are, in fact, two big spinules inserted on the coxa and, therefore, are not homologous to the ornamentation present in the ingroup 5. However, even considering a widespread occurrence of a similar ornamentation within the family, it is clear that the presence of such character is a unique autapomorphy for a more derived monophylum within *Remaneicaris* and certainly do not compose the groundpattern of the genus.

It seems that there is a correspondence between the size of the enp of males' leg 4, with the size of the spinules near the insertion of the endopod and with the degree of thickness of the cuticle near the insertion of these spinules. For example, in the *cordobaensis*-group nov., when the enp is small, less hirsute and relatively thin (viz. *R. sierrae*, *R. cordobaensis* and *R. ciliata*), thus, there is an absence of the row of spinules near the insertion of the endopod, as well as an absence of the low cuticularized zone. Within the same group, in *R. sanctiludovici* the endopod is as big as the exp 1, with a very well cuticularized zone and a row of spinules over it. The same can be observed in the

persephone-group nov. The only exception seems to occur in *R. rhizophora*, although in Noodt's (1965) drawings, it seems that, on this species, the endopod is a short segment with a very long distal seta. It is not clear what is/are the functions of this(ese) structures, although we can speculate that the spinules on the basis, over the low cuticularized zone give some reinforcement for strong and very flexible endopodites.

Other species within Parastenocarididae also have a row of spinules near the insertion of the endopod, such as the groups *brevipes* and *minuta*. A row of spinules can be seen also in the *nana*-group. In accordance with Lang (1948), the group *brevipes* should be closely related the *muscicola*-group, due to their strong developed enp of males leg 4. The group *minuta* should be also related to the *brevipes*-group, while the group *nana* should be closer to the *minuta*-group, experiencing as a major evolutionary novelty, the loss of the enp of the leg 4 of males. I am not sure about a closer kinship between the *brevipes* and the *minuta/nana* groups, although all of them have a row of spinules near the insertion of the enp (or where it should be; in the case of the *nana*-group). Thus, it is still difficult to say which position they occupy within the family and if we should consider the presence of spinules on the basis of the leg 4 of males, near the insertion of the endopod, as an autapomorphy for a bigger group of species. Even if they occupy the basis of the cladogram within the outgroup 1, we should consider this ornamentation near the endopod insertion as appearing at least two times within the family, since in *Remaneicaris*, this character do not compose its groundpattern. A low cuticularized zone have not been found in any of these groups mentioned above, or have not been figured. But it seems that this character is also unique to the ingroup 5, not appearing outside the genus.

The presence of a modified seta on the 9th segment of males A1 is also one of the most distinctive features present at this level and can be seen in all species within ingroup 5. It appears as a proximal dilatation of the innermost seta of male A1. In the other species within the genus, this

seta shows a normal shape and in the *analuizae*-group nov. it appears as an inner seta, separated from the others by the distal hyaline margin. The presence of this modified seta have never been described for other species of Parastenocarididae and probably evolved only once within the family.

Within ingroup 5, the *tridactyla*-group nov. can be characterized by the presence of 2 up to 6 strong spinules on the ventral side of the telson, at the basis of furca (char. 30). Within *Remaneicaris* a primary homologous ornamentation can be seen also in all members of the *analuizae*, *persephone* and *cordobaensis* group nov. Despite of the positional homology, only in the *tridactyla*-group nov. these spinules are well developed, appearing as a small row of weakly developed spinules in other groups within the ingroup 4.

Another autapomorphy of the *tridactyla*-group nov. is the presence of a row of spinules on the dorsal margin of the telson, before the insertion of the sensilla (char. 45). This character have been found also in *R. ciliata*, *R. itacambirucui* n. sp., *R. persephone* and in females of *R. sierrae*. However, the presence of other characters such as A1 of males with a hyaline region in *R. itacambirucui* and the presence of a leg 6 with two setae in *R. ciliata*, *R. persephone* and *R. sierrae*, makes clear that these are independent occurrences within the genus.

Besides these derived characters, the *tridactyla*-group nov. can be considered the most basal taxon within the ingroup 5, retaining the higher amount of plesiomorphies at this level. For example, all members of this group have retained the characters 35, 36 and 37. Other very interesting plesiomorphies of this group is the absence of leg 6 armed with two seta and the presence of a dorsal integumental window on the 2nd urosomite.

The presence of an armed leg 6 is an autapomorphy for a taxon formed by the groups *cordobaensis* and *persephone* (char. 42). As already mentioned in a previous paper (Corgosinho *et al.* 2007), although the presence of armature on leg 6 may be considered a plesiomorphic condition, the most parsimonious assumption is to consider the appearance of these elements as an

autapomorphy for a more derived group within *Remaneicaris*, since the alternative would imply the loss of this character at least four times within the genus. To explain the appearance *de novo* of a plesiomorphic structure, previously lost in the ground pattern of the family, we need to understand how homeobox genes control patterns of limbs development after the hatching of the larvae. In this sense I believe that the reappearance of an armed leg 6 in the *cordobaensis/persephone* group nov. can be due to the suppression of a homeobox gene repressor at the level of the second urosomite.

The splitting of the dorsal integumental window of the second urosomite (char. 14, st. 3) in two lateral windows is one of the most characteristic autapomorphies of the *persephone*-group nov., together with a female endopod of leg 4 bigger than the exp 1 (char. 29). In what concerns the size of leg 4 endopod in females, a similar condition also occurs within the *analuzae*-group nov., in *R. divae*. In the *persephone*-group nov., the female of *R. oncophora* is unknown. However, in view of the presence of this character in all species within this group, here I have chosen, in the phylogeny, to consider it as present in this species.

Due to the variability found in the structure of male leg 3 in *Remaneicaris*, it was sometimes difficult to find and polarize some characters and even after, most of them turned out to be plesiomorphies. In this sense, it is very interesting the presence of characteristic proximal distension (char. 43) on the inner margin of males leg 3 in the *cordobaensis*- group nov.

The *P. ahaggarica* problem

Remaneicaris species share as a synapomorphy, the subdistal position of the outer seta of leg 4, as well as some clear plesiomorphies such as an endopod of the leg 3 of males and the first endite of Mx2 with two setae. Outside *Remaneicaris*, only *P. ahaggarica*, from Algeria, have these characters and therefore, could be included in *Remaneicaris*, within the *argentina*-group nov., sharing with *R. argentina* and *R. drepanephora* the characteristic endopod of male leg 4, the shape

of leg 5, the apparent hyaline margin on the apophysis of the leg 3 of males and the modified distal spinule on the exp 1 of the same limb. Considering this, and the geographic occurrence of this species, it is difficult to not include it within *Remaneicaris*. However, the presence of a long spinule on the inner margin of enp 1 of leg 1 rises some questions about the close relationship of *P. ahaggarica* with *R. argentina* and *R. drepanephora*. Furthermore, there is no description about the relative position of the leg 5, or any information about the presence or absence of an intercoxal sclerite. Also, there is no information about the presence and position of the integumental windows. At the moment, and considering the aberrant Mx1 described by Bozic (1978) together with the lack of detailed information, it is also difficult to be sure about the position of *P. ahaggarica* as a member of *Remaneicaris*.

The family is present in all continents, with the exception of Antartida, Tasmania islands and New Zealand (Schminke, 1981). In the light of these facts it is reasonable to think that, if in the future, this species turned out to belong to *Remaneicaris*, thus, the genus should be considered gondwanic. Therefore, under this circumstance, the sister group of *Remaneicaris* need to be looked for in Africa, India, or in the Neotropical region.

P.S.: Due to the similarity between females of Parastenocarididae, this key is mostly based on male characters. *Incerta sedis* species were not included and their identification deserve future studies.

Key for identification of *Remaneicaris* species

- 1- Leg 4 with outer spine in a subdistal position; Mx2 with two setae on the proximal endite; Exp 2 and 3 of legs 2 and 4 with long medial spinule on the outer margin.....***Remaneicaris*_2**
- Without this combination of characters.....**other Parastenocarididae**

2 (1)- Basis of leg 1 with a seta on the inner margin in both sexes; basis without outer seta in both sexes; cuticle thick and perforated; dorsal integumental window on urosomites 2-5 of males and 2- 4 of females; exp 1 of leg 4 with the proximal row of spinules linearly arranged; endopod of males leg 4 bilobed on inner margin and with a distal hyaline seta.....***R. ignotus***

- Without this combination of characters..... **3**

3 (2)- Basis of leg 1 without inner seta; leg 1 enp 1 with an inner row of spinules in males; basis of male leg 4 without ornamentation, endopod short, outwardly curved, with spinules on the outer side and a hyaline region on the inner concave margin; male leg 3 exopod straight; thumb making 180° with the exp.....***R. meyerabichi***

- Basis of leg 1 without inner seta; leg 1 enp 1 without inner row of spinules on both sexes; leg 3 of males with hyaline apophysis and a modified distal spinule on the outer margin; enp 2 of leg 4 smooth, without any ornamentation on the inner margin***argentina -group_7***

- Basis of leg 1 without inner seta; leg 1 enp 1 with an inner row of spinules on both sexes; enp 2 of leg 4 ornamented with a row of spinules on the inner margin.....**4**

4 (3)- Last segment of males A1 with a hyaline margin near the insertion of the aesthetasc.....***analuizae - group_12***

- Last segment of male A1 without a hyaline margin near the insertion of the aesthetasc and with a modified seta; basis of male leg 4 with a proximal inner row of strong spinules.....**5**

5 (4) - Telson with a row of strong spinules ventrally, near the insertion of the furca; dorsally, with a paraopercular row of spinules before the insertion of the sensilla.....***tridactyla – group_16***

- Leg 6 armed with setae or spines.....**6**

– Without this character, but with one laterodorsal window on each side of the body.....*persephone*-group_23

6 (5) - Male leg 3 with a proximal inner expansion.....*cordobaensis* – group_20

– second urosomite with one laterodorsal window on each side of the body.....*persephone* – group_23

argentina -group

7 (3) - Distal modified spinule of exp 1 of male leg 3 without a hyaline margin.....8

– with a hyaline margin.....9

8 (7)- Endopod of leg 4 of males outwardly curved, short (not reaching the half of the exp 1), hirsute on the inner margin, with very small spinules on the proximal region and long spinules distally arranged; thumb curved; distal spinule is shorter than thumb.....*R. clanestina*

– Endopod of male leg 4 outwardly curved, short (not reaching the half of the exp 1), hirsute, with a row of long spinules along proximal margin; thumb straight; distal spinule straight, long, of the same size as thumb.....*R. palaciosi*

9 (7) - Male leg 3 endopod longer than 2/3 of the exopod.....10

– Much shorter.....11

10 (9) - Male leg 3 without a row of spinules proximally on the outer margin.....*R. hurdi*

– With a row of strong spinules proximally.....*R. jujuyensis*

11 (9) - Thumb shorter than apophysis.....*R. drepanephora*

– Thumb very long, ca. two times bigger than apophysis; endopod of male leg 4 very long, of the same size as exp 1 and with long spinules on inner margin.....*R. argentina*

analuizae - group

12 (4)- Paraopercular region not ornamented with spinules; inner margin of the basis of the leg 3 of males with long spinules; thumb with a hyaline margin; male leg 4 endopod long, almost as long as exp 1, ornamented with some (3) long spinules proximally and distally with some short spinules.....*R. ivoneae*

- paraopercular margin ornamented with spinules.....**13**

13 (12)- Male leg 3 exopod with a proximal row of spinules and a distal row of very long spinules (setules); thumb with hyaline margin; telson with row of spinules on the dorsal margin, before the insertion of the sensilla.....*R. itacambirucui*

- Telson with a linear row of spinules running ventrally along the proximal region.....**14**
- Telson with two ventral patches of spinules on each side of the proximal region; male leg 3 with spinules proximally on the inner margin of the exopod.....**15**

14 (13)- Telson with linear row of ventral spinules of equal size running along the proximal region; integumental window of the last urosomite splitted in two laterodorsal windows on each side of the somite; second urosomite with two dorsolateral windows; basis of males leg 3 with outer spinules, endopod oval, with distal spinules.....*R. insolitus*

- Telson with a linear ventral row of spinules of irregular size; furca very long (almost as long as the telson and the last urosomites combined); paraopercular ornamentation continuous with ventral row of spinules near the insertion of the furca; thumb very long and straight; apophysis with hyaline bud.....*R. divae*

15 (13)- Male leg 3 with endopod; anterior margin of furca dilated and anteriorly with a semicircular row of spinules; two dorsal patches of spinules on each side of the last urosomite; dorsal row of spinules along distal rim of operculum.....*R. tageae*

- Without endopod.....**16**

16 (15) - Male leg 2 with a bilobed endopod; basis of male leg 3 with a proximal process on the inner margin; proximal margin of the exopod inwardly expanded.....*R. euniceae*

- Urosomites 4 and 5 of males and 3 and 4 of females with lateral integumental windows; basis of male leg 3 with hyaline spinule on inner margin.....*R. analuizae*

tridactyla - group

16 (5) - Thumb triphid.....**17**

- Without this character.....**18**

17 (16) - Telson, ventrally with big spinules near insertion of furca; male leg 3 endopod with two subdistal spinules and without seta.....*R. tridactyla*

- Telson, ventrally with up to 5-6 big spinules near insertion of furca; male leg 3 endopod with a distal seta.....*R. paratridactyla*

18 (16) - Male leg 4 endopod hirsute; basis with a low cuticularized margin near insertion of the endopod.....**19**

- Leg 4 endopod of males not hirsute, resembling the leg 2 in some aspects; male leg 3 endopod foliaceous, with a row of spinules on inner margin; thumb with a hyaline margin.....*R. paraensis*

19 (18) - Male leg 3 apophysis surrounded by hyaline margin; very strong spinules near the insertion of leg 4 endopod in males.....*R. paraguayensis*

- Telson with dorsal ornamentation on the last two urosomites.....*R. juliae*

- Thumb modified, with a subdistal process upwardly curved; telson with paraopercular ornamentation and with row of very strong spinules on dorsal margin, before the operculum.....*R. remanei*

***cordobaensis* - group**

20 (6)- Male leg 4 endopod long, as long as exp 1; long spinules near the insertion of endopod; outer margin of endopod with stronger spinules than in inner margin; long spinules (setules) near the distal outer margin of males leg 3.....*R. sanctiludovici*

- Without spinules near insertion of the endopod of male leg 4.....**21**

21 (20) - Basis of male leg 3 with an inner row of long spinules.....**22**

- Basis of the 3 of males without ornamentation; thumb serrated on the inner margin.....*R. sierrae*

22 (21) - Thumb with hyaline inner margin.....*R. cordobaensis*

- without this character.....*R. ciliata*

***persephone* - group**

23 (6) - Male leg 3 without endopod (reduced to a seta); exopod with very long apophysis, bigger than the thumb and with a proximal depression.....*R. oncophora*

- Male leg 3 with endopod.....**24**

24 (23) - exopod with short apophysis and with a proximal depression.....*R. pluto*

- Basis of male leg 4 without a poorly cuticularized margin near the insertion of endopod.....**25**
- With a poorly cuticularized margin near the insertion of the endopod.....**26**

25 (24) - Apophysis hypertrophied, inwardly curved in more than 90°, endopod oval with subterminal spinules; leg 4 endopod short (less than 1/3 of expodite 1), hirsute on the inner margin and with distal hyaline margin, basis with row of spinules adjacent to insertion of endopod.....*R. membranacea*

- leg 4 endopod short, with a very long setae, hirsute on both sides crossing the distal rim of exp 1.....*R. rhizophora*

26 (24) - Thumb with inner hyaline margin; endopod of males leg 3 hirsute along its margin.....*R. hecate*

- Thumb with blunt tip; endopod of males leg 3 with distal spinules.....*R. persephone*

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Table 1 (continuation) - Matrix for cladogram in figure 1 (selected characters for the used outgroups; from left to right, characters from A to X).

| Taxa | Caracteres |
|----------------------------------|------------------------|
| <i>Psammonitocrella</i> | 1111111110000000000000 |
| Outgroup_01 | 1111100001111111111111 |
| <i>R. meyerabichi</i> | 1111100001111111111111 |
| <i>R. palaciosi</i> | 1111100001111111111111 |
| <i>R. jujuyensis</i> | 1111100001111111111111 |
| <i>R. ignotus</i> | 1111100011111111111111 |
| <i>R. rhizophora</i> | 1111100001111111111111 |
| <i>R. cordobaensis</i> | 1111100001111111111111 |
| <i>R. ciliata</i> | 1111100001111111111111 |
| <i>R. sierrae</i> | 1111100001111111111111 |
| <i>R. membranacea</i> | 1111100001111111111111 |
| <i>R. sanctiludovicci</i> | 1111100001111111111111 |
| <i>R. argentina</i> | 1111100001111111111111 |
| <i>R. clandestina</i> | 1111100001111111111111 |
| <i>R. drepanephora</i> | 1111100001111111111111 |
| <i>R. paraensis</i> | 1111100001111111111111 |
| <i>R. icoaraci</i> | 1111100001111111111111 |
| <i>R. paraguayensis</i> | 1111100001111111111111 |
| <i>R. remanei</i> | 1111100001111111111111 |
| <i>R. analuizae</i> | 1111100001111111111111 |
| <i>R. euniceae</i> | 1111100001111111111111 |
| <i>R. insolitus</i> sp.nov. | 1111100001111111111111 |
| <i>R. itacambirucui</i> sp.nov. | 1111100001111111111111 |
| <i>R. ivoneae</i> sp.nov. | 1111100001111111111111 |
| <i>R. tridactyla</i> sp.nov. | 1111100001111111111111 |
| <i>R. paratridactyla</i> sp.nov. | 1111100001111111111111 |
| <i>R. juliae</i> sp.nov. | 1111100001111111111111 |
| <i>R. tageae</i> | 1111100001111111111111 |
| <i>R. divae</i> | 1111100001111111111111 |
| <i>R. hurdi</i> | 1111100001111111111111 |
| <i>R. pluto</i> | 1111100001111111111111 |
| <i>R. hecate</i> | 1111100001111111111111 |
| <i>R. oncophora</i> | 1111100001111111111111 |
| <i>R. persephone</i> | 1111100001111111111111 |

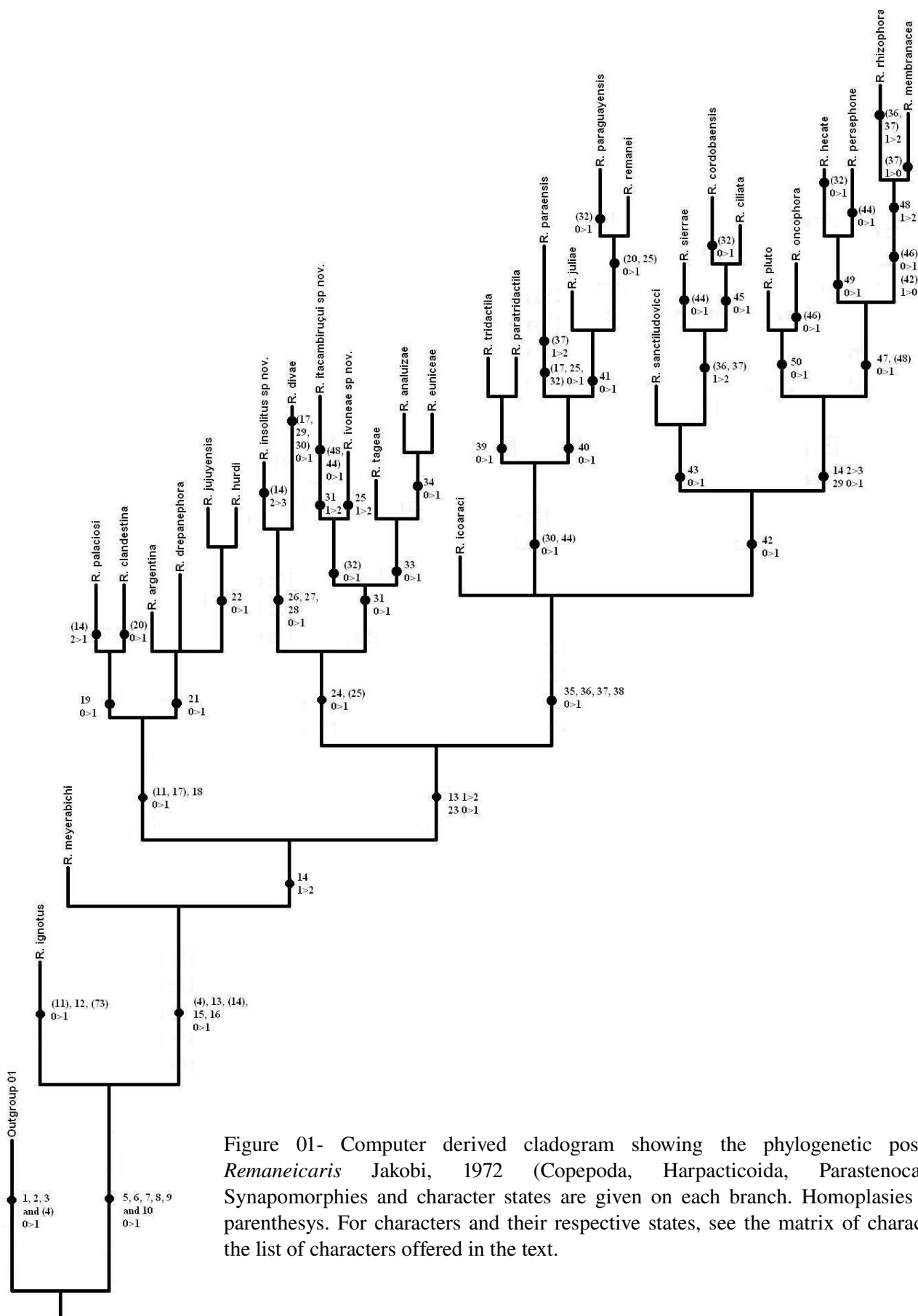


Figure 01- Computer derived cladogram showing the phylogenetic position of *Remaneicaris* Jakobi, 1972 (Copepoda, Harpacticoida, Parastenocarididae). Synapomorphies and character states are given on each branch. Homoplasies between parenthesis. For characters and their respective states, see the matrix of characters and the list of characters offered in the text.

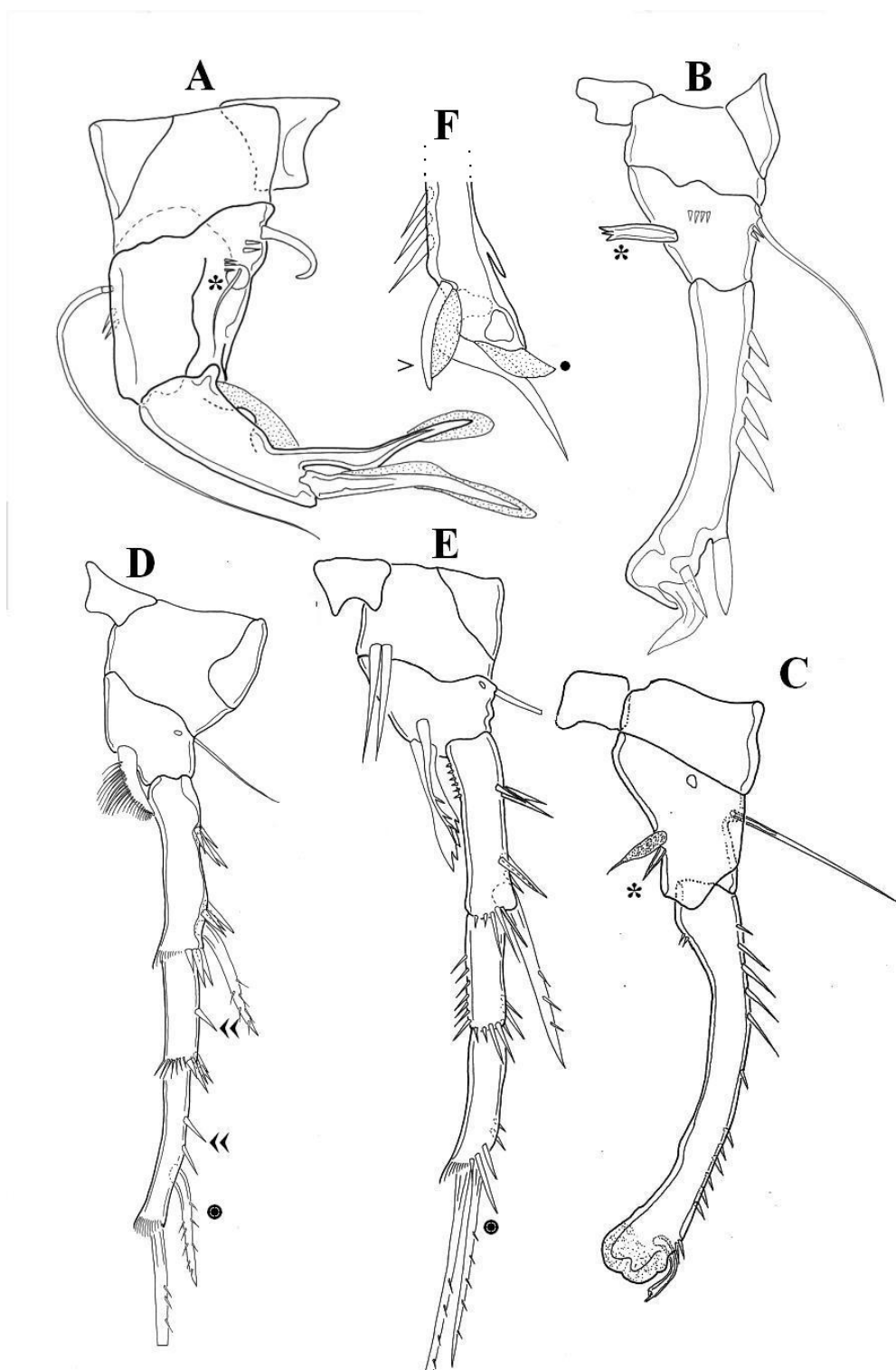


Figure 02- Leg 3 of a male of *Brasilibathynellocaris salvadorensis* (Noodt, 1965), A; *Remaneicaris juliae* Corgosinho, Martínez Arbizu and Santos Silva, 2007, B and *Remaneicaris euniceae* Corgosinho and Martínez Arbizu, 2005, C. Leg 4 of a male of *R. palaciosi* (Noodt, 1962), D; *Murunducaris dactyloides* (Kiefer, 1967), E and *R. jujuyensis* (Noodt, 1965), F. Symbols identifies homologies and/or synapomorphies between the appendices. Figures are out of scale.

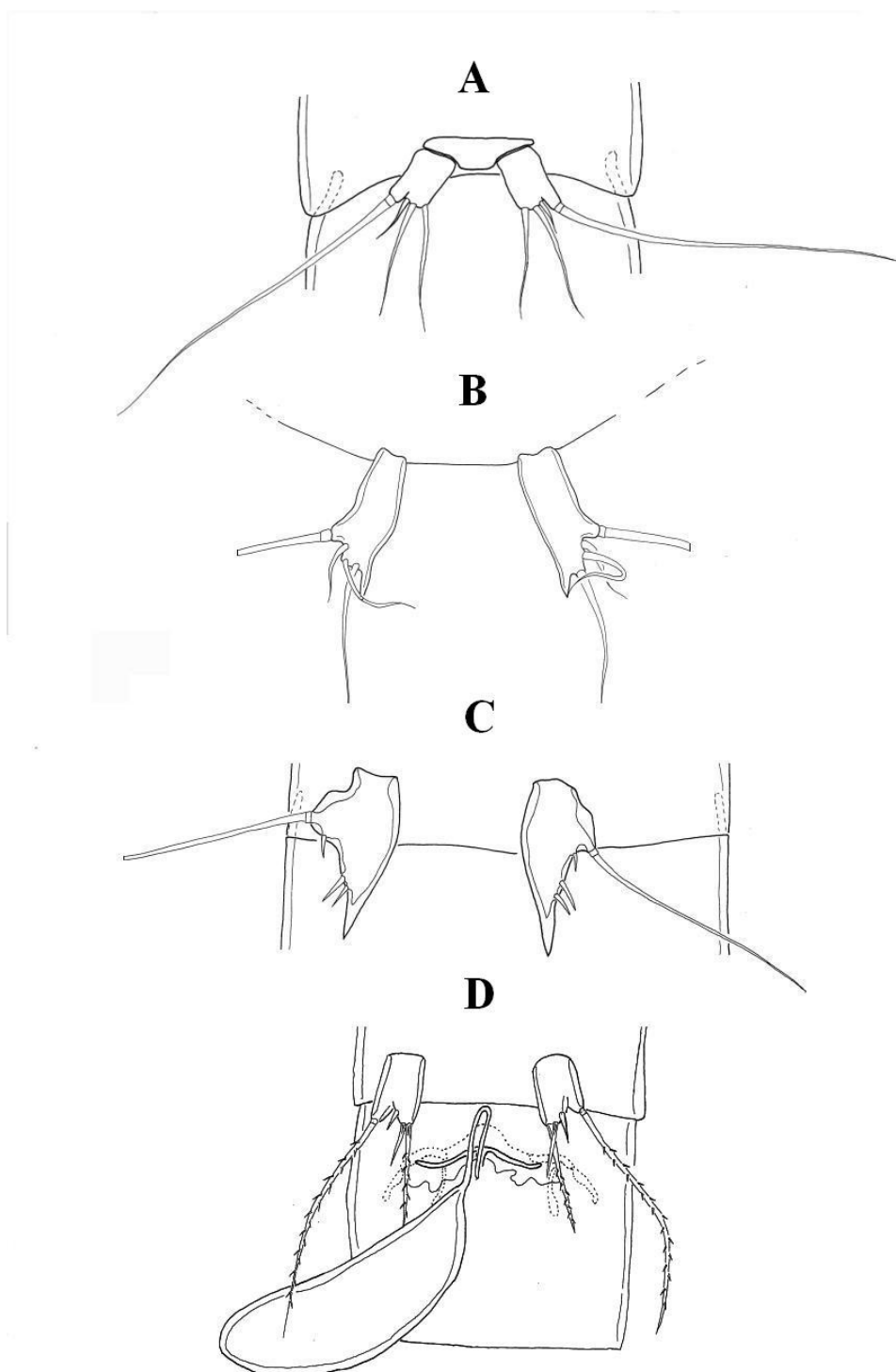


Figure 03- Leg 5 of a male of *Remaneicaris ignotus* (Dussart, 1983), A; *R. argentina* (Noodt, 1965), B; *R. tridactyla* Corgosinho, Martínez Arbizu and Santos Silva, 2007, C and of a female of *R. analuizae* Corgosinho and Martínez Arbizu, 2005, D. Figures out of scale.

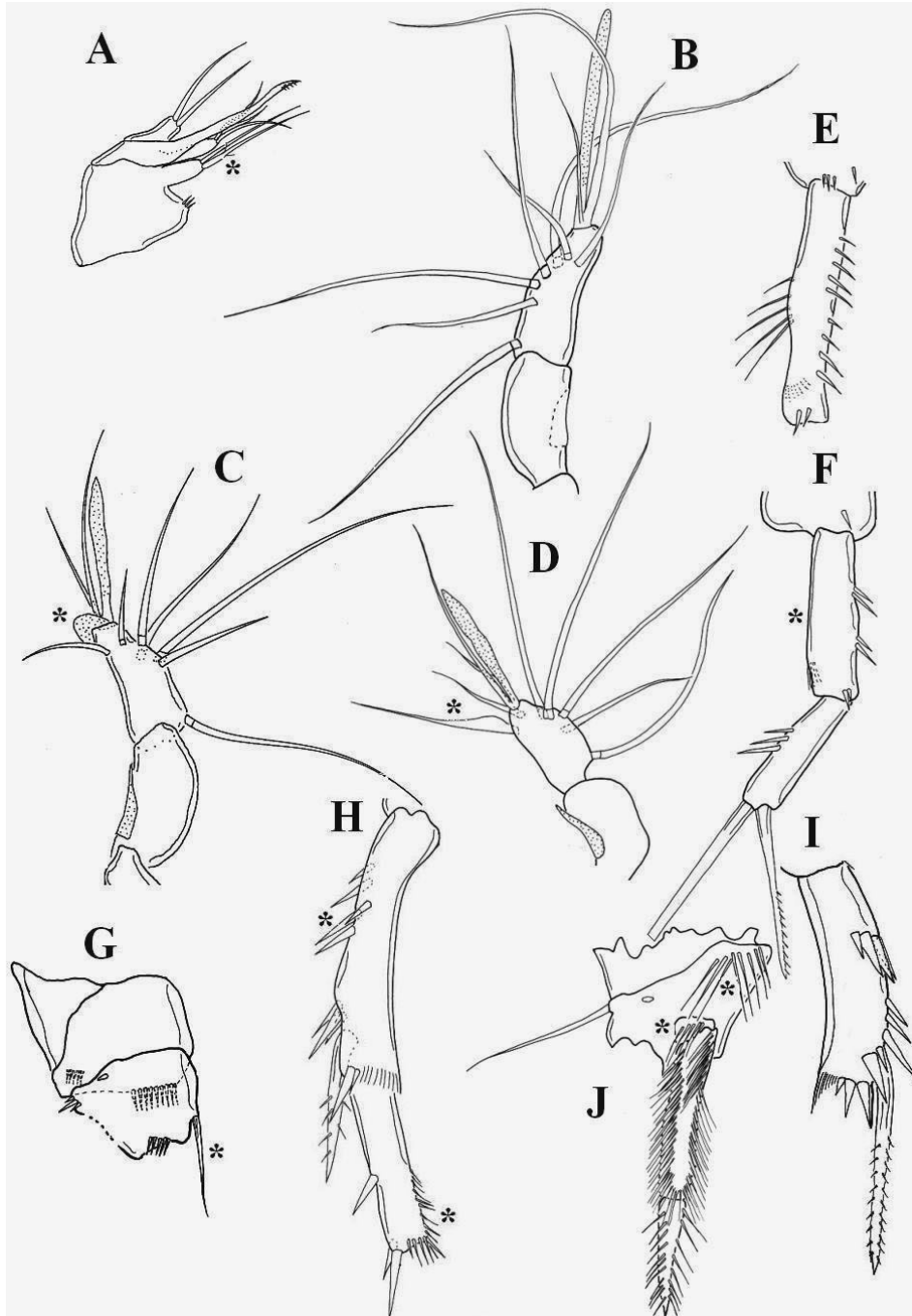


Figure 04- A, Mx2 of *R. analuizae* Corgosinho and Martínez Arbizu, 2005, , B, segments 8 and 9 of the A1 of males of *R. ignotus* (Dussart, 1983); C, A1 of *R. analuizae* Corgosinho and Martínez Arbizu, 2005, males; D, A1 of *R. oncophora* (Noodt, 1965) males; E, enp 1 from the leg 1 of *R. oncophora* (Noodt, 1965) males; F, enp 1 from the leg 1 of *R. jujuyensis* (Noodt, 1965) males; G, coxa and basis from leg 1 of *R. ignotus* (Dussart, 1983) males; H, exp 1 and 2 of the leg 4 of males of *R. oncophora* (Noodt, 1965); J, leg 4 basis and enp of *R. oncophora* (Noodt, 1965) males. Symbols identifies homologous and/or synapomorphies. Figures are out of scale.

Chapter VI

Noodt's and Kiefer's *Remaneicaris* Jakobi (Copepoda, Harpacticoida, Parastenocarididae)

species: Redescription of the species and discussion of characters present within each monophyletic groups.

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Abstract

Remaneicaris is a very speciose monophyletic group from the neotropis, easily characterized by the subdistal position of the outer seta of the third exopodite of leg 4. The group retains an unusual set of plesiomorphic characters, being composed by 31 species accommodated in five monophyletic groups, plus *R. ignotus* and *R. meyerabichi*. In this work we redescribe most of the species previously described for the neotropis and a brief comment about the evolutionary tendencies within each monophyletic group is given.

Keywords: Copepoda, Parastenocarididae, *Remaneicaris*, redescription, Neotropis.

Introduction

⁴¹ Manuscript on the format of the journal “Zootaxa”.

The Neotropical Parastenocarididae fauna is very rich in species, being composed by different monophyletic groups from various evolutionary tendencies. Within the South and Central America we can find some much derived groups such as *Murunducaris* and *Brasilibathynellocaris*, as well as the genus *Remaneicaris*, the most basal group within the family.

The first studies of South American Parastenocarididae started with Menzel (1916), with the description of *Parastenocaris staheli* Menzel, 1916 from Surinam and Delachaux (1924), which described *P. chelifera* Delachaux, 1924 also from Surinam. For *Remaneicaris*, the first described species was *R. hexacantha* (Kiefer, 1936), from the Northeast of Brazil. Later, Jakobi and Silva (1962) described *R. hurdi* (Jakobi and Silva, 1962) from the South of Brazil, while Noodt (1962) described *R. palaciosi* (Noodt, 1962) and *R. meyerabichi* (Noodt, 1962) from Central America. One year later, in a monograph entitled “Subterrane Crustaceen der zentralen Neotropis”, Noodt (1963) created the *remanei*-group. However, even for Noodt (1965, 1969), there were some doubts about the “monophyly” of the group (i.e. “*Diese group erweist sich als in sich noch inhomogen und wird in Zukunft eine weitere Differenzierung erfordern*” Noodt 1965). Only in 1972 the genus *Remaneicaris* was created by Jakobi (1972), in order to group some species placed by Noodt (1963, 1965 and 1972) in the *remanei*-group.

However, some of the species previously included by Noodt (1963, 1965 and 1972) in the *remanei*-group were excluded from the genus *Remaneicaris* by Jakobi (1972), while others, from different evolutionary tendencies, were added to this genus by this author. As a consequence, the result was a polyphyletic genus, never accepted by other authors. Recently, Corgosinho and Martínez Arbizu (2005) redefined the genus *Remaneicaris* and provided a new diagnosis based also in synapomorphies. Critics about the non adoption of this genus as well as the other genera created by Jakobi (1972) can be seen in Corgosinho (chapter 5).

Today the fauna of parastenocaridids encompasses circa of 241 species and subspecies (Corgosinho *et al.* 2007). With 34⁵ species, the genus *Remaneicaris* is the most speciose Neotropical group of Parastenocarididae. However, this can be more an effect of sampling than a solid pattern for the region.

The genus retain an unusual set of plesiomorphic characters, and can be divided in five monophyletic groups (Corgosinho chapter 5), plus *R. ignotus* (Dussart, 1983) and *R. meyerabichi* (Noodt, 1962).

In this work we redescribe most of the species of the genus *Remaneicaris* and some morphological tendencies are briefly discussed.

Material and Methods

The type material of the species redescribed in this work was loaned from the Noodt's collection deposited in the Deutsches Zentrum für Marine Biodiversitäts Forschung, from the Senckenberg Forschungsinstitut und Naturmuseum (Germany) and from Kiefer's collection at the Landesamtes für Naturkunde of Karlsruhe (Germany). Most of Noodt's preparations contain more than one specimen, thus, sometimes it was impossible to know the type. In these cases, the material was worked as a syntype and the best appendices were drew. Drawings were made using a drawing tube on a Leica DMR microscope, equipped with Normarsky interference contrast, at 400x and 1000x magnification.

Abbreviations used are: A1 = antennule, A2 = antenna, Ae = aesthetasc, Md= mandible, Mx1= Maxillulae, Mx2= Maxillae, Mxp= maxilliped, enp= endopod, exp= exopod, P1-P5 = legs 1 to 5, PRS= proximal row of spinules, DRS= distal row of spinules, PEHZ= pre endopodal hyaline zone, IBRS= inner basal row of spinules, RVS= row of “V” spinules.

⁵² Sensu Corgosinho and Martínez Arbizu (2005), plus the following species included in this PhD: *R. tridactyla*, *R. paratridactyla*, *R. juliae*, *R. ivoneae*, *R. itacambirucui* and *R. insolitus*.

Some of the species that appears here could not be redrawn in details due to the bad state of some of the preparations. In these cases we proceed to the redescription only comparing the original text and drawings with what we saw. The type species of *Remaneicaris psammae* (Rouch, 1962) and *R. hurdi* were not found and thus, these species are not redescribed here. The type material of *Remaneicaris divae* (Noodt, 1972) and *R. tageae* (Noodt, 1972) are almost lost and were only checked for characters. Thus, these species are not redescribed here as well.

Descriptive part

Family Parastenocarididae Chappuis, 1940

Genus *Remaneicaris* Jakobi, 1972

Species *Remaneicaris meyerabichi* (Noodt, 1962).

References and synonyms: *Parastenocaris meyer-abichi* Noodt, W. 1962, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris meyerabichi* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris meyerabichi* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris meyer-abichi* Dussart, B. and Defaye, D., 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris meyerabichi* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; S175 (locus typicus).

Locus typicus: River Zacatiapa, in the road San Salvador to Zacatecoluca.

Male- Length 370-380 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax, 2nd and 5th urosomites with 1 dorsal integumental window each. Telson without ornamentation (Fig. 1). Anal operculum smooth and convex. Furca (Fig. 1) with 7 setae. All setae located in distal third. A1 9-segmented and haplocer; armature

beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 2 C) coxa unarmed; basis with outer seta and 1 pore on the anterior margin, 3 spinules on the outer margin, and 2 distally, between the insertion of the enp; enp 2-segmented, segment 1 with 1 row of 3 long spinules along the inner side and 2 groups of 3 spinules on the outer margin; segment 2 with 3 spinules on the inner margin, two on the outer margin and 2 setae distally, 1 of them geniculated; exp 3-segmented, segment 1 with outer spine, segment 2 unarmed, segment 3 with 2 outer spines, 2 geniculated setae and a posterior pore; Leg 2 (Fig. 2 D) coxa unarmed; basis without outer seta, ornamented with 1 row of spinules on outer margin and 1 pore near the anterior margin; exp 3-segmented, the first segment being approximately of the same size of the remaining exp, with a proximal row of spinules distributed in as soft “v”, on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules (the innermost are smaller than the outermost spinules); segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented with 1 subdistal seta and a big distal spinule. Leg 3 (Fig. 2 A) coxa unarmed; basis with outer seta; enp spiniform, 1-segmented; exp 1-segmented, straight, with some spinules irregularly distributed on the outer margin; apophysis short, without additional cuticularization and with a very small process on the inner margin; thumb is long, with a s-curvature on the proximal third and straight on the distal 2/3. Leg 4 (Fig. 2 B) coxa unarmed; basis with outer seta and one pore on anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of spinules distributed in a soft “v” shape (RVS), a row of spinules anterior to the insertion of the outer spine

and an inner hyaline frill; segment 2 without setae, with a row of spinules distally (innermost spinules are smaller than the outermost) and with one long spinule located mesially at the outer side; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill and two spinules located on the outer margin; enp 1-segmented, short, outward curved, with numerous spinules on the distal third of the inner margin, concave margin with a hyaline area. Leg 5 rectangular, ending in an small process on the inner margin.

Female- Sexually dimorphic in A1, leg 1, leg 2, leg 3, leg 4 and genital field.

Length 390 μm (Noodt's measurement). Rostrum as in male. Cephalothorax and double genital somite and 4th urosomite with 1 dorsal integumental window each. Telson and furca as in male. A1 7-segmented; number of setae beginning at proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 as in male. Leg 1 without an inner row of spinules on the inner margin of the exp 1. Leg 2 (Fig. 3 B) coxa unarmed, with a posterior row of spinules; basis and exp as in male; enp with a subdistal seta, three distal spinules and a row of two spinules on the outer margin. Leg 3 (Fig. 3 C) coxa unarmed; basis with 1 outer seta, and ornamented with 1 row of spinules near the insertion of the enp; exp 2-segmented, segment 1 with an outer spine, a proximal row of spinules, a row of spinules next to the outer spine and a row of spinules distally, on the inner margin (on the place of the hyaline frill), segment 2 with 1 spine and 1 seta; enp 1-segmented and spiniform, with 2 spinules on the outer margin. Leg 4 (Fig. 3 A) basis with a row of spinules near the enp insertion; exp as in male, enp spine-like, with 1 row of 4 spinules on the anterior margin and two spinules on the middle, between the separation of the enp and the incorporated distal seta. Leg 5 as in male. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Genus *Remaneicaris* - *analuizae* group⁶

Species *Remaneicaris argentina* (Noodt, 1965).

References and synonyms: *Parastenocaris argentina* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4(2): 84-129; *Remaneicaris argentina* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris argentina* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris argentina* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris argentina* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C137 (M3, slide 11; locus typicus and M3, slide 12).

Locus typicus: Rio Sierra (La Bolsa), in the mountain between the city of Córdoba and Alta Gracia (Carretera), Córdoba- Argentina.

Male- Length 450 μ m (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax and 2nd urosomites with 1 dorsal integumental window each. Fifth urosomite with one lateral windows on each side of the somite. Anal operculum smooth and slightly concave. Furca as described by Noodt (1965), with 7 setae; all of them located in the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 coxa unarmed; basis with outer seta and 1 pore on the anterior margin, 3 spinules on the outer margin; enp 2-segmented, segment 1 without ornamentation on the inner margin; segment 2 with 4 spinules on the inner margin, 2 on the outer margin and 2 setae distally, 1 of them geniculated; exp 3-segmented,

⁶³ A formal definition of each monophyletic group within *Remaneicaris* can be seen in the manuscript about phylogeny (chapter 5).

segment 1 with outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 4 A) coxa unarmed; basis without outer seta, ornamented with 1 row of spinules on outer margin and 1 pore near the anterior margin; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules of unequal sizes; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented with 1 subdistal seta, two distal spinules and two spinules on the outer margin. Leg 3 (Fig. 4 B) coxa unarmed; basis with outer seta; enp spiniform, 1-segmented; exp 1-segmented, straight, with a proximal row of strong spinules on the outer margin, distally, with two very strong spinules, the distalmost with a hyaline lamella on the inner margin; apophysis with a hyaline margin; thumb is long, inwardly curved on the proximal third and almost straight on the distal 2/3. Leg 4 (Fig. 4 C) coxa unarmed; basis with outer seta and one pore on anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an outer spine inserted posteriorly; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a row of spinules distally (innermost spinules are smaller than the outermost) and with one long spinule located mesially at the outer side; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill and two spinules located on the outer margin; enp 1-segmented, long, slender and with numerous spinules on the inner margin. Leg 5 (Fig. 4 E) rectangular, ending in a small process on the inner margin.

Female: Sexually dimorphic in A1, leg 3, leg 4 and genital field.

Length 450 μm (Noodt's measurement). Rostrum as in male. Cephalothorax and double genital somite with 1 dorsal integumental window each. Fourth urosomite with one lateral windows on each side. Telson and furca as in male. A1 7-segmented; number of setae beginning at proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 as in male. Leg 1 as in males (Fig. 5 A). Leg 3 (Fig. 5 B) coxa unarmed; basis with 1 outer seta; exp 2-segmented, 1st segment with a proximal row of spinules, an outer spine, a row of spinules next to the outer spine and a row of spinules distally, on the inner margin (on the place of the hyaline frill); segment 2 with 1 spine and 1 seta; enp 1-segmented and spiniform, with 2 spinules on the beginning of the 3rd/4th of the segment. Leg 4 (Fig. 5 C) basis with a row of spinules near the enp insertion; exp as in male, enp spine-like, with 2 small spinules on the inner margin and two bigger spinules on the outer margin. Leg 5 as in male. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris jujuyensis* (Noodt, 1965).

References and synonyms: *Parastenocaris jujuyensis* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4(2): 84-129; *Remaneicaris jujuyensis* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris jujuyensis* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris jujuyensis* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris jujuyensis* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C134 (M3, slide 7; locus typicus).

Locus typicus: Quebra Honda, 3 km north of Jujuy, Jujuy-Argentina.

Male- Length 420 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax with 1 dorsal integumental window. Anal operculum

smooth and slightly concave, with a small protuberance on each side of the paraopercular region, just above the furca. Furca as described by Noodt (1965), with 7 setae; all of them located in the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 6 A) coxa unarmed; basis with an outer seta, 1 pore and 3 spinules on the outer margin; additionally with one spinule between the exp and the enp; enp 2-segmented, segment 1 without ornamentation on the inner margin; segment 2 with 3 spinules on the inner margin and 2 setae distally, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 6 B) coxa unarmed; basis without outer seta, ornamented with 1 row of spinules and 1 pore on the outer margin; distally, on the inner margin, with a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules of unequal sizes; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, long, straited proximally, approximately of the same size of the exp 1, with 1 long and spinulous distal seta, two subdistal spinules and four spinules on the outer margin. Leg 3 (Fig. 7 A) coxa unarmed; basis with outer seta; enp very long, dagger-like, almost of the same size of the whole exp, 1-segmented, with a row of spinules proximally, on the inner margin; exp 1-segmented, straight, with a row of 4 big spinules proximally and 4 distally; last spinule very modified, with a hyaline lamella on the inner margin; apophysis short, ending in a hyaline precess; thumb is long, strong and curved (s-shaped).

Leg 4 (Fig. 7 B) coxa unarmed; basis with outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an outer spine inserted posteriorly; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a row of spinules distally (innermost spinules are smaller than the outermost) and with one long spinule located mesially at the outer side; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and two spinules located on the outer margin; enp 1-segmented, very short, concave on the outer margin and with a row of spinules along the inner and convex margin. Leg 5 (Fig. 7 C) rectangular, ending in a small process on the inner margin, as previously described by Noodt (1965).

Female: Sexually dimorphic in A1, leg 2, leg 3, leg 4, leg 5 and genital field.

Length 360 μm (Noodt's measurement). Rostrum as in male. Integumental windows probably as in males. Telson and furca as in male. A1 7-segmented; number of setae beginning at proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 as in male. Leg 2 enp slightly weaker than the enp of males, appearing as a long appendix with long distal setae and 3 spinules on the outer margin. Leg 3 coxa unarmed; basis with 1 outer seta and a row of spinules near the insertion of the enp; exp 2-segmented, 1st segment with a proximal row of spinules, an outer spine, two big spinules near to the outer spine and a row of spinules distally, on the inner margin (on the place of the hyaline frill); segment 2 with 1 spine, 1 seta and one spinule displaced mesially, on the outer margin; enp 1-segmented and spiniform, with 2 spinules on the middle. Leg 4 not observed; probably as described by Noodt (1965), without sexual dimorphism on the exp; Leg 5 almost as in male, but with a bigger inner process. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris drepanephora* (Kiefer, 1967).

References and synonyms: *Parastenocaris drepanephora* Kiefer, F. 1967, Amazoniana 1(2): 131-134; *Remaneicaris drepanephora* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris drepanophora* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris drepaneophora* Dussart, B. 1984, Hydrobiologia 113: 25-67; *Parastenocaris drepanophora* Rouch, 1986, In: Botosaneanu, L. , Stygo fauna Mundi: 321-355; *Parastenocaris drepanophora* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Parastenocaris drepanephora* Reid, J. 1998, Catalogue of Crustacea of Brazil: 75-127; *Remaneicaris drepanephora* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: The whole type series deposited in the Kiefer's collection at the Karlsruhe museum (Germany)⁷⁴.

Locus typicus: Rio tapajós, near the city of Santarém (Pará- Brazil)

Male- Length 365 µm from rostrum until the distal rim of telson (in accordance with Kiefer 1967, the size range vary between 340-380 µm from rostrum until telson). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax and 2nd urosomite with 1 dorsal integumental window. Fifth urosomite with a lateral integumental window on each side of the segment. Anal operculum smooth and slightly concave (Fig. 8 A and B). Furca with 7 setae (Fig. 8 A and B); all of them located in the distal third. A1 (Fig. 9 A) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 (Fig. 9 C) with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in

⁷⁴ In accordance with Kiefer 1967, the type material is deposited at the Instituto nacional de pesquisas da Amazônia (INPA-Brazil), but it is in fact deposited in the Karlsruhe University Museum.

R. analuizae; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 9 B) coxa unarmed; basis with an outer seta, 1 pore and 4 spinules on the outer margin; additionally with 2 spinules between the exp and the enp; enp 2-segmented, segment 1 without ornamentation on the inner margin; segment 2 with 2 spinules on the inner margin, 2 on the outer margin and 2 setae distally, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 10 A) coxa unarmed, with two spinules on the posterior margin; basis without outer seta, ornamented with 1 row of spinules and 1 pore on the outer margin; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and 3 spinules located on the outer margin. Leg 3 (Fig. 10 B) coxa unarmed, with a row of spinules on the posterior margin; basis with outer seta; enp short, spine-like and without ornamentation; exp 1-segmented, straight, with a row of 4 big spinules proximally and 4 distally; last spinule very modified, with a hyaline lamella on the inner margin; apophysis short, ending in a hyaline precess; thumb is shorter than apophysis, ending in a blunt tip. Leg 4 (Fig. 10 C) coxa unarmed; basis with outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an outer spine inserted posteriorly; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a row of spinules distally (innermost spinules are smaller than the outermost) and with one long spinule located mesially on the outer margin; segment 3 with 1 apical and 1 subdistal outer

seta, a distal hyaline frill on the inner margin and two spinules located on the outer margin; enp 1-segmented, approximately half the side of the exp 1; with two distinct rows of spinules on the inner margin, covering its distal half; the proximalmost row is composed by bigger spinules. Leg 5 rectangular, ending in a small process on the inner margin.

Female: Sexually dimorphic in A1, leg 3, leg 4, furca and genital field.

Length 360 μm , from cephalotorax until the distal rim of telson. Rostrum as in male. For sensila see figure 11 B. Dorsal integumental windows on cephalotorax and double genital somite; lateral on the 4th urosomite. Telson as in male (Fig. 11 A and B). Furca with 7 setae (Fig. 11 A); all of them located in the distal third; sexually dimorphic, with a proximal, a more medial and distal rows of spinules on the dorsal side (Fig. 11 A). A1 7-segmented; number of setae beginning at proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 as in male. Leg 3 (Fig. 12 A) coxa unarmed; basis with 1 outer seta, an outer pore and a row of spinules on the posterior margin; exp 2-segmented, 1st segment with a proximal row of spinules, an outer spine, a row of spinules before the insertion of the outer spine and a row of spinules distally, on the inner margin (on the place of the hyaline frill); segment 2 with 1 spine, 1 seta and one spinule displaced mesially, on the outer margin; enp 1-segmented and spiniform, with 1 spinules on the outer margin. Leg 4 enp dimorphic (Fig. 12 B), spiniform, with two anterior spinules turned to the inner margin, two more posterior spinules on the outer margin and some alternated spinules displaced distally, probably being part of the incorporated seta. Leg 5 (Fig. 12 C) as in male. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris palaciosi* (Noodt, 1962).

References and synonyms: *Parastenocaris palaciosi* Noodt, W. 1962, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris palaciosi* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris palaciosi* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris palaciosi* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris palaciosi* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; S64 (locus typicus), S127, S332 (K7, slides 7-8).

Locus typicus: Acehuafa river (San Salvador, El Salvador).

Male- Length 420 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax and 2nd urosomite with 1 dorsal integumental window. Fifth urosomite with a belt-like integumental window running dorsally until the lateral sides. Anal operculum smooth (Fig. 13) and quadratic. Furca (Fig. 13) with 7 setae; all of them located in the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 14 A) coxa unarmed; basis with an outer seta, 1 anterior pore and 4 spinules on the outer margin; additionally with 3 spinules at the level of the enp; enp 2-segmented, segment 1 without ornamentation on the inner margin; segment 2 with 3 spinules on the outer margin and 2 setae distally, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 14 B) coxa unarmed; basis without outer seta, with

1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules of unequal sizes; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules placed on the distal third of the segment. Leg 3 (Fig. 15 A and B) coxa unarmed; basis with outer seta; enp spiniform, short, without ornamentation or armature; exp 1-segmented, slightly curved, with a row of 4 big spinules proximally and 3 distally; last spinule very strong and almost straight, without any hyaline structure on it; apophysis short, ending in a hyaline precess; thumb is long, strong and almost straight. Leg 4 (Fig. 15 C) coxa unarmed; basis with outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an outer spine inserted posteriorly; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a row of spinules distally (innermost spinules are smaller than the outermost) and with one long spinule located mesially at the outer side; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp shorter than the half of the exp 1, outwardly curved and with small spinules along the inner margin. Leg 5 rectangular (Fig. 16 B), ending in an small process on the inner margin.

Female: Sexually dimorphic in A1, leg 3, leg 4 and genital field.

Length 440 μm (Noodt's measurement). A1 7-segmented; number of setae beginning at proximal segment: 0/4/5/2+Ae/1/2/9+Ae. Leg 3 (Fig. 16 A) coxa unarmed; basis with 1 outer seta, an anterior

pore and a row of spinules near the insertion of the enp; exp 2-segmented, 1st segment with a proximal row of spinules, an outer spine, two big spinules near to the outer spine and a row of spinules distally, on the inner margin (on the place of the hyaline frill); segment 2 with 1 spine, 1 seta and one spinule displaced mesially, on the outer margin; enp 1-segmented and spiniform, with 2 outer spinules displaced in the middle of the segment. Leg 4 exp without sexual dimorphism; enp 1-segmented, with two outer spinules and a distal, unincorporated spine (Fig 15 D). Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris clandestina* (Noodt, 1963).

References and synonyms: *Parastenocaris clandestina* Noodt, W. 1963, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris clandestina* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris clandestina* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris clandestina* Dussart, B. 1984, Hydrobiologia 113: 25-67; *Parastenocaris clandestina* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris clandestina* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Parastenocaris clandestina* Reid, J. 1998, Catalogue of Crustacea of Brazil: 75-127; *Remaneicaris clandestina* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; P270 (locus typicus; M2, slides 18 and 20) and P275 (M3, slide 2).

Locus typicus: Hyporheic zone of the margin of the Amazon river, on the city of Santarém (Pará, Brazil).

Male- Length 290 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Integumental windows not seen in Noodt's preparations. Anal operculum smooth and slightly convex. Furca with 7 setae; all of them located in the distal third; inner margin with of the furca with an strong concavity. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 coxa unarmed; basis with an outer seta, 1 anterior pore and 4 spinules on the outer margin, enp 2-segmented, segment 1 without ornamentation on the inner margin; segment 2 with 2 distal setae, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 coxa unarmed; basis without outer seta, with 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a softly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules. Leg 3 (Fig. 17 C and D) coxa unarmed; basis with outer seta; enp filiform, short, without ornamentation or armature; exp 1-segmented, slightly courved, with a proximal row of 3 big spinules proximally and 2 distal spinule; last spinule very strong and curved; without any hyaline structure on it; apophysis short, ending in a hyaline precess, preceded by a chitinous plate; thumb is long, strong and heavily curved in a "S" shape. Leg 4 coxa unarmed; basis with outer seta and one pore on the anterior margin; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an

outer spine inserted posteriorly; proximally with a softly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a row of spinules distally and with one long spinule located mesially at the outer side; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp (Fig. 17 E) shorter than the half of the exp 1, outwardly curved and with small spinules along the inner margin (proximally with very small spinules). Leg 5 rectangular, ending in a small process on the inner margin.

Female: Sexually dimorphic in A1, leg 3, leg 4 and genital field.

Length 300-310 μm (Noodt's measurement). A1, leg 3, leg 4 and genital field as in *R. palaciosi*.

Ingroup 5 (viz. Corgosinho chapter 5)

Species *Remaneicaris icoaraci* (Noodt, 1963).

References and synonyms: *Parastenocaris icoaraci* Noodt, W. 1963, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris icoaraci* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris icoaraci* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris icoaraci* Dussart, B. 1984, Hydrobiologia 113: 25-67; *Parastenocaris icoaraci* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris icoaraci* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Parastenocaris icoaraci* Reid, J. 1998, Catalogue of Crustacea of Brazil: 75-127; *Remaneicaris icoaraci* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; P279 (M2, slides 1-3 and 5).

Locus typicus: Groundwater of the Amazon river, near the city of Icoaraci (Pará, Brazil).

Male- Length 380 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment. Anal operculum smooth and slightly convex. Furca with 7 setae; all of them located in the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 coxa unarmed; basis with an outer seta, 1 anterior pore and 4 spinules on the outer margin, enp 2-segmented, segment 1 with a row of spinules on the inner margin; segment 2 with 2 distal setae, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 coxa unarmed; basis without outer seta, with 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially, on the outer margin and with a row of distal spinules; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules. Leg 3 coxa unarmed; basis with outer seta; enp unisegmented and with a distal seta; exp 1-segmented, almost straight, with a row of strong spinules along the outer margin; apophysis short, rounded, without hyaline margin; thumb (Fig. 17 B) is strong and scythe shaped. Leg 4 (Fig. 17 A) coxa unarmed; basis with outer seta, one pore on the anterior margin and a strong row of spinules on the inner margin (IBRS); distally, with a

row of spinules and a low chitinized zone (PEHZ) near the insertion of the enp; exp 3-segmented, segment 1 almost of the same size of the remaining segments and with an outer spine inserted posteriorly; proximally with a strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules, one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp leaf shaped, with long spinules on the outer margin and a distal spine. Leg 5 triangular, ending in a strong process on the inner margin; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp and genital field.

Length 340-350 μm (Noodt's measurement). A1 and leg 3 without any special modification, like in the other species previously described. Leg 4 exp as in males; enp like in the species described before. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

***Tridactyla*-group**

Species *Remaneicaris remanei* (Noodt, 1963).

References and synonyms: *Parastenocaris remanei* Noodt, W. 1963, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris remanei* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris remanei* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris remanei* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris remanei* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris remanei* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C257 (M4, slides 7-10).

Locus typicus: Groundwater of the Ypacarai Lake (San Bernardino, Paraguay).

Male- Length 470 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment (Fig. 18). Last urosomite with a dorsal row of spinules on the distal margin. Telson (Fig. 18) ornamented, with a proximal row of spinules on the dorsal side (PRS), a distal row of strong spinules of unequal size near the operculum (DRS), a paraopercular ornamentation and a row of strong spinules ventrally, near the insertion of the furca. Anal operculum quadratic. Furca with 7 setae; all of them located in the distal third; proximally constrained. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 19 A) coxa unarmed, with a posterior row of spinules; basis with an outer seta, 1 anterior pore, 3 spinules on the outer margin and 3 spinules distally arranged; enp 2-segmented, segment 1 with a row of long spinules on the inner margin; segment 2 with a row of outer spinules and 2 distal setae, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 19 B) coxa unarmed, with two spinules on the posterior margin; basis without outer seta and with a posterior row of spinules, 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one

spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and five outer spinules. Leg 3 (Fig. 19 C) coxa unarmed; basis with outer seta; enp unisegmented and filiform; exp 1-segmented, almost straight on the outer margin and with two strong rows of 5-6 spinules each; inner margin with irregular border and with a strong invagination; distally with a strong lameliform process somehow detached from the main axis; apophysis quadratic; thumb is strong, with a distal process. Leg 4 (Fig. 19 D) coxa unarmed; basis with outer seta, one pore on the anterior margin and IBRS; distally, with a row of spinules and a PEHZ near the insertion of the enp; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp leaf shaped and completely hirsute. Leg 5 triangular, smaller than in female and ending in a strong process on the inner margin; all setae outwardly placed (Fig. 19 E).

Female: Sexually dimorphic in A1, leg 3, leg 4 enp and genital field.

Length 440-470 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 enp somehow more slender than in the other species. Leg 4 exp as in males; enp slender and hirsute (Fig. 19 F). Leg 5 triangular and stronger than in males. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris paraguayensis* (Noodt, 1963).

References and synonyms: *Parastenocaris paraguayensis* Noodt, W. 1963, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris paraguayensis* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris paraguayensis* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris paraguayensis* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris paraguayensis* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris paraguayensis* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C257 (M4, slides 1-4; locus typicus); C258 (M2, slide 14).

Locus typicus: Groundwater of the Ypacarai lake (San Bernardino, Paraguay).

Male- Length 440 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment (Fig. 20 A and B). Last urosomite with a dorsal row of spinules on the distal margin. Telson (Fig. 20 B) ornamented on the dorsal side, with a ARS, a PRS with spinules of unequal size, a paraopercular row of 2 strong spinules and a row of strong spinules ventrally, near the insertion of the furca. Anal operculum concave. Furca almost of the same size of the telson, with 7 setae; all of them located in the distal third; with a strong invagination along the inner margin (viz. Noodt 1963, figure 121). A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+ Ae/1/4/2/9+ Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 21 A) coxa unarmed,

with a posterior row of spinules; basis with an outer seta, 1 anterior pore, 3 spinules on the outer margin and 3 spinules distally arranged; enp 2-segmented, segment 1 with a row of long spinules on the inner margin; segment 2 with a row of outer spinules and 2 distal setae, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 21 B) coxa unarmed, with two spinules on the posterior margin; basis without outer seta and with a posterior row of spinules, 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules. Leg 3 (Fig. 21 C) coxa unarmed; basis with outer seta; enp unisegmented, comb like, with a row of spinules along the inner margin; exp 1-segmented, slightly curved, with an outer row of 6 strong spinules and a distal row of two strong spinules separated by three very small spinules; apophysis rounded, with a hyaline margin; thumb is strong, curved and with an inner hyaline margin. Leg 4 (Fig. 21 D) coxa unarmed; basis with outer seta, one pore on the anterior margin and IBRS; distally, with a row of spinules and a strong PEHZ near the insertion of the enp; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one

big spinule mesially placed on the outer margin; enp leaf shaped and completely hirsute. Leg 5 triangular and ending in a strong process on the inner margin; all setae outwardly placed (Fig. 21 E).

Female: Sexually dimorphic in A1, leg 3, leg 4 enp and genital field.

Length 420-440 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in *R. icoaraci*. Leg 4 exp as in males; enp spiniform, with three outer spinules. Leg 5 as in males. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Variability: *Remaneicaris paraguayensis* f. *phyloides* (Noodt, 1963).

Female length: 440- 470 (Noodt's measurement): Cephalic and thoracic appendices as in the forma "typica". Telson and last urosomite ornamentation like in males (Noodt 1963, figure 117 and 118). Furca hypertrophied, with all setae distally arranged.

Species *Remaneicaris paraensis* (Noodt, 1963).

References and synonyms: *Parastenocaris paraensis* Noodt, W. 1963, Beiträge zur Neotropischen Fauna 2(3): 143-248; *Remaneicaris paraensis* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris paraensis* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris paraensis* Dussart, B. 1984, Hydrobiologia 113: 25-67; *Parastenocaris paraensis* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris paraensis* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Parastenocaris paraensis* Reid, J. 1998, Catalogue of Crustacea of Brazil: 75-127; *Remaneicaris paraensis* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; P279 (M2, slides 1-4; locus typicus); C258 (M2, slide 14).

Locus typicus: Groundwater of the Amazon river, near the city of Icoaraci (Pará, Brazil).

Male- Length 450 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment (Fig. 22 A and B). Telson (Fig. 22 B) ornamented on the dorsal side, with a PRS with small spinules, a paraopercular row of 2 small spinules and a row of spinules ventrally, near the insertion of the furca. Anal operculum quadratic. Furca circa of 2.5x longer than wide (Fig. 22 B and Noodt 1963, figure 106), slightly oval in dorsal view and with 7 setae, all of them located in the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta (Fig. 23 A). A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 23 B) coxa unarmed, with a posterior row of spinules; basis with an outer seta, 1 anterior pore, 3 spinules on the outer margin and 2 spinules distally arranged; enp 2-segmented, segment 1 with a row of long spinules on the inner margin; segment 2 with a row of outer spinules and 2 distal setae, 1 of them geniculated; exp 3-segmented, segment 1 with an outer spine, segment 2 unarmed, segment 3 with 2 outer spines and 2 geniculated setae. Leg 2 (Fig. 24 A) coxa unarmed, with two spinules on the posterior margin; basis without outer seta and with a posterior row of spinules, 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin

and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules. Leg 3 (Fig. 24 B) coxa unarmed; basis with outer seta; enp unisegmented, comb like, with a row of spinules along the inner margin; exp 1-segmented, slightly curved, with an outer row of 10-12 strong spinules along the entire outer margin; apophysis spatuliform and longer than wide; thumb longer than apophysis, slightly curved and with an inner hyaline margin. Leg 4 (Fig. 24 C) coxa unarmed; basis with outer seta, one pore on the anterior margin, an IBRS and a distal row of spinules near the insertion of the enp; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp somehow similar to the enp of the leg 2, but without the subdistal seta, with a hyaline distal edge, three spinules on the inner margin, three distally, on the posterior side and one in the anterior side, also distally arranged. Leg 5 bilobbed, with all exopodal setae distally placed (Fig. 24 D).

Female: Sexually dimorphic in A1, leg 3, leg 4 enp and genital field.

Length 450 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in *R. icoaraci* (Fig. 25 A). Leg 4 exp as in males; enp spiniform, with spinules along the outer margin. Leg 5 as in males. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Variability: *Remaneicaris paraensis* f. *bulbifera* (Noodt, 1963).

Female Length 440- 450 μm (Noodt's measurement): Cephalic and thoracic appendices as in the forma "typica". Telson ornamentation like in males (Fig. 25 B). Furca hypertrophied (Fig. 25 B) with all setae distally arranged.

Species *Remaneicaris hexacantha* (Kiefer, 1936).

References and synonyms: *Parastenocaris hexacantha* Kiefer, F. 1936, Zoologischer Anzeiger 116: 142-144; *Remaneicaris hexacantha* Lang, K. 1948, Monographie der Harpacticiden vol 2: 1682 pp.; *Parastenocaris hexacantha* Noodt, W. 1955. Archiv für Hydrobiologie 50(1): 76-81; *Parastenocaris hexacantha* Chappuis, P. A. 1957. Vie et Milieu 8: 423-432; *Parastenocaris hexacantha* Jakobi, H. 1959. Revista Brasileira de Biologia 19(3): 271-286; *Parastenocaris hexacantha* Jakobi, H. 1960. Revista Brasileira de Biologia 20(3): 327-358; *Parastenocaris hexacantha* Jakobi, H. 1962. Boletim da Universidade Federal do Paraná, Zoologia, 1(21): 1-92; *Parastenocaris hexacantha* Jakobi, H. and Loyola e Silva, J. 1962. Proceedings of the United States National Museum 113(3458): 389-397; *Parastenocaris hexacantha* Jakobi, H. 1969. Boletim da Universidade Federal do Paraná, Zoologia, 3(7): 167-191; *Parastenocaris hexacantha* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris hexacantha* Löffler, H. 1981, In: Hurlbert, S. H. *et al.*, Aquatic biota of tropical South America, Part I, Arthropoda: 14-19; *Parastenocaris hexacantha* Dussart, B. 1984, Hydrobiologia 113: 25-67; *Parastenocaris hexacantha* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris hexacantha* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Parastenocaris hexacantha* Reid, J. 1998, Catalogue of Crustacea of Brazil: 75-127; *Remaneicaris hexacantha* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: The whole type series deposited in the Kiefer's collection at the Karlsruhe museum (Germany).

Locus typicus: Rio Seridó (Paríba, Brazil)

Male unknown. Female- Length 380 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment (Fig. 26). Telson (Fig. 26) ornamented on the dorsal side, with a strong DRS, a paraopercular row of 3 strong spinules and a row of up to 5 strong spinules ventrally, near the insertion of the furca. Anal operculum quadratic. Furca is modified, of the *truncata* type (similar to the furca of *Brasilibathynellocaris panamericana truncata* (Noodt, 1962)), with 7 setae, all of them located in the distal third; setae 4 and 5 extremely reduced and with a wide basis (ornamented distally with numerous spinules) (Fig. 26). A1 7-segmented; armature beginning with proximal segment: 0/4/5/2+Ae/1/2/9+Ae. A2 like in the other species previously described. Md, Mx1, and Mxp armature as in *R. analuizae*; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 as in the other females of the tridactyla group, with an inner row of spinules on the enp 1 (Fig. 27 A). Leg 2 (Fig. 27 B) coxa unarmed; basis without outer seta and with 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal

spinules and two outer spinules. Leg 3 (Fig. 27 C) coxa unarmed; basis with outer seta; enp spiniform with one outer spinules; exp as in the other previously described females. Leg 4 (Fig. 27 D) coxa unarmed; basis with outer seta, one pore on the anterior margin and a distal row of spinules near the insertion of the enp; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp spiniform, of the same size of the exp 1 and with two outer spinules. Leg 5 triangular, with a strong inner process; all exopodal setae laterally placed (Fig. 27 E).

***Cordobaensis*-group**

Species *Remaneicaris cordobaensis* (Noodt, 1965).

References and synonyms: *Parastenocaris cordobaensis* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris cordobaensis* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris cordobaensis* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris cordobaensis* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris cordobaensis* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C137 (M3, slides 15-16; locus typicus).

Locus typicus: Groundwater of the Rio Sierra (Córdoba, Argentina).

Male- Length 440 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment. Telson without ornamentation. Anal operculum smooth and convex. Furca with 7 setae. All setae located on the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1 (Fig. 28 A). Leg 2 (Fig. 28 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and five outer spinules. Leg 3 (Fig. 28 C) coxa unarmed; basis with outer seta and an inner row of long spinules; enp unisegmented, with the distal seta incorporated to the segment; exp 1-segmented, inwardly curved, weakly ornamented on the outer margin and with a strong inner process on the proximal third; apophysis rounded, weakly chitinized on the distal rim; thumb is strong, short, smaller than the apophysis, curved and with an inner hyaline margin. Leg 4 (Fig. 28 D) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine

inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is short, not reaching the half of the exp1, with a row of spinules along the inner margin and distally. Leg 5 triangular and ending in a strong process on the inner margin; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp; leg 6 and genital field.

Length 430 μm (420-440 μm ; Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group. Leg 4 exp as in males; enp spiniform, almost of the same size as the exp 1. Leg 6 as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris ciliata* (Noodt, 1965).

References and synonyms: *Parastenocaris ciliata* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris ciliata* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris ciliata* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris ciliata* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris ciliata* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C137 (M3, slides 18 and 20; locus typicus) and C135 (M3, slide 19).

Locus typicus: Groundwater of the Rio Sierra (Córdoba, Argentina).

Male- Length 430 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment. Telson without ornamentation (Fig. 29). Anal operculum smooth and convex. Furca with 7 setae and a dorsal row of 3 spinules on the dorsal side (Fig. 29). All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 30 A) with a row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 30 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and four outer spinules. Leg 3 (Fig. 30 D) coxa unarmed; basis with outer seta and an inner row of long spinules; enp unisegmented, with the distal seta incorporated to the segment; exp 1-segmented, inwardly curved, weakly ornamented on the outer margin and with a strong inner process on the proximal third; apophysis rounded, weakly chitinized on the distal rim; thumb is

strong, short, smaller than the apophysis and curved. Leg 4 (Fig. 30 C) as in *R. cordobaensis*. Leg 5 triangular and ending in a strong process on the inner margin; all setae outwardly placed.

Female: Sexually dimorphic in furca, A1, leg 3, leg 4 enp; leg 6 and genital field.

Length 400-420 μm (Noodt's measurement). Furca (Fig. 31 A), in lateral view, with an oval shape, with all setae inserted distally and with a continuous row of spinules along the dorsal side. A1 without any special modification, like in the other species previously described. Leg 2 as in males (Fig. 30 E). Leg 3 as in the other species of the group. Leg 4 exp as in males; enp spiniform (Fig. 30 F), almost of the same size as the exp 1, with three spinules inserted in the medial region. Leg 5 as in males (Fig. 32). Leg 6 (Fig. 32) as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris sierrae* (Noodt, 1965).

References and synonyms: *Parastenocaris sierrae* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris sierrae* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris sierrae* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris sierrae* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris sierrae* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C137 (M3, slides 13-14; locus typicus).

Locus typicus: Groundwater of the Rio Sierra (Córdoba, Argentina).

Male- Length 430 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalotorax and 2nd urosomite; last

urosomite with one lateral window on each side of the segment. Telson without ornamentation. Anal operculum smooth and convex. Furca with 7 setae (Fig. 33). All setae located in distal third.

A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 34 A) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and three outer spinules. Leg 3 (Fig. 34 B) coxa unarmed; basis with outer seta; enp unisegmented, with the distal seta incorporated to the segment; exp 1-segmented, inwardly curved, weakly ornamented on the outer margin and with a strong inner process on the proximal third; apophysis is rounded, well chitinized; thumb is strong, short, smaller than the apophysis and inwardly curved. Leg 4 (Fig. 34 C) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the

innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is proportionally longer than in *R. cordobaensis*, *R. sierrae* and *R. ciliata*, passing the first half of the exp 1 and with long spinules along the outer and inner margin. Leg 5 triangular and ending in a strong process on the inner margin; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp; leg 6 and genital field.

Length 430 µm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group. Leg 4 exp as in males; enp spiniform, almost of the same size as the exp 1. Leg 6 as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris sanctiludovici* (Noodt, 1965).

References and synonyms: *Parastenocaris sanctiludovici* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris sanctiludovici* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris sanctiludovici* Rouch, 1986, In: Botosaneanu, L. , Stygo fauna Mundi: 321-355; *Parastenocaris sanctiludovici* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris sanctiludovici* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C139 (M1, slides 15-16; locus typicus); C132 (M1, slide 11).

Locus typicus: River of unknown name in the Pampa, circa of 7 kilometers from the city of San Luiz in the province of San Luiz (Argentina).

Male- Length 440 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental windows on cephalothorax and 2nd urosomite; last urosomite with one lateral window on each side of the segment. Telson (Fig. 35) without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae (Fig. 35). All setae located on the distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 36 A) as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 36 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and four outer spinules. Leg 3 (Fig. 37 A) coxa unarmed; basis with outer seta; enp unisegmented; exp 1-segmented, inwardly curved, with a row of spinules along the proximal half of the outer margin and with bigger spinules near the insertion of the thumb (one of them is very long); apophysis is rounded, well chitinized; thumb is strong, short, smaller than the apophysis and inwardly curved. Leg 4 (Fig. 37 B) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules and a PEHZ; exp 3-segmented, segment 1 almost of the same size of the

remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is long (almost of the same size as the exp 1), hirsute, leaf shaped, with spinules along the outer and inner margin (outer spinules are stronger than the inner spinules). Leg 5 triangular and ending in a strong process on the inner margin; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp; leg 6 and genital field.

Length 440- 460 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group. Leg 4 (Fig. 37 C) exp as in males; enp spiniform, almost of the same size as the exp 1. Leg 5 as in males (Fig. 38). Leg 6 (Fig. 38) as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

***Persephone*-group**

Species *Remaneicaris persephone* (Noodt, 1965).

References and synonyms: *Parastenocaris persephone* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris persephone* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris persephone* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris persephone* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384;

Remaneicaris persephone Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, *Senckenbergiana Biologica* 85(2): 147-162.

Observed material: Noodt collection; C138 (M1, slides 4 and 8; locus typicus).

Locus typicus: River Cuatro (Córdoba, Argentina).

Male- Length 480 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window on cephalothorax; 2nd urosomite with a double latero dorsal windows (resulting from the splitting of the original dorsal window); last urosomite with one lateral window on each side of the segment. Telson with a distal row of spinules near the operculum. Anal operculum smooth and quadratic. Furca with 7 setae. All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 39 A) as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 39 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and three outer spinules. Leg 3 (Fig. 40 A) coxa unarmed; basis

with outer seta; enp unisegmented, with four distal spinules and one spinule in subdistal position; exp 1-segmented, inwardly curved, with a row of four strong spinules on the proximal third and three spinules near the insertion of the thumb (the middle spinule is very strong); apophysis is rounded, longer than larger and well chitinized; thumb is strong, longer than the apophysis and with a blunt tip. Leg 4 (Fig. 40 B) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules and a PEHZ; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is long, passing the first half of the exp 1, completely hirsute and leaf shaped. Leg 5 (Fig. 40 C) triangular and with an inner process; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp; leg 5, leg 6 and genital field.

Length 460- 490 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 2 as in males (Fig. 41 A). Leg 3 as in the other species of the group (Fig. 41 B). Leg 4 (Fig. 41 C) exp as in males; enp spiniform, blade shaped, longer than exp1 and with an outer row of four spinules. Leg 5 with a strong inner process, as usual for this group, conferring a triangular shape to this limb. Leg 6 as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris hecate* (Noodt, 1965).

References and synonyms: *Parastenocaris hecate* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris hecate* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris hecate* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris hecate* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris hecate* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C138 (M1, slides 17-18; locus typicus); C138 (M1, slides 1-2).

Locus typicus: River Cuatro (Córdoba, Argentina).

Male- Length 510 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window (Fig. 42 A) on cephalothorax; 2nd urosomite with a double latero dorsal windows (resulting from the splitting of the original dorsal window); last urosomite with one lateral window on each side of the segment. Telson without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae (Fig. 42 B). All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 43 A) as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 43 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner

hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and five outer spinules. Leg 3 (Fig. 44 A) coxa unarmed; basis with outer seta; enp unisegmented, with spinules along almost the entire margins, conferring to it a brush shape; exp 1-segmented, inwardly curved, with a row of seven strong spinules on the proximal half and five spinules along the second half; apophysis is rounded, longer than larger and well chitinized; thumb is strong, longer than the apophysis and with a pointed tip and with a hyaline membrane along its inner margin. Leg 4 (Fig. 44 B) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules and a PEHZ; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is long, passing the first half of the exp 1, completely hirsute and leaf shaped. Leg 5 triangular and with an inner process; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp, leg 6 and genital field.

Length 480- 500 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group (Fig. 45 A). Leg 4 (Fig. 44 C) exp as in males; enp spiniform, blade shaped, longer than exp1 and with an outer row of four

spinules. Leg 6 (Fig. 45 B) as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris pluto* (Noodt, 1965).

References and synonyms: *Parastenocaris pluto* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris pluto* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris pluto* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris pluto* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris pluto* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C138 (M1, slide 20; locus typicus); C138 (M1, slide 3).

Locus typicus: River Cuatro (Córdoba, Argentina).

Male- Length 360 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window (Fig. 46 A) on cephalothorax; 2nd urosomite with a double latero dorsal windows (resulting from the splitting of the original dorsal window); last urosomite with one lateral window on each side of the segment. Telson without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae (Fig. 46 B). All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 47 A) as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 47 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior

pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and two outer spinules. Leg 3 (Fig. 47 C) coxa unarmed; basis with outer seta; enp unisegmented, with a long distal flagellum; exp 1-segmented, straight, with a row of four spinules on the proximal half and one spinule on the second half; apophysis is quadratic, short, appearing after a distal depression at the level of the thumb; thumb is strong, slightly longer than the apophysis and with a blunt tip. Leg 4 (Fig. 47 D) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules and a PEHZ; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is long, passing the first half of the exp 1, completely hirsute and leaf shaped. Leg 5 triangular and with an inner process; all setae outwardly placed (Fig. 47 E).

Female: Sexually dimorphic in A1, leg 3, leg 4 enp, leg 6 and genital field.

Length 340- 360 μm (Noodt's measurement). A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group. Leg 4 (Fig. 46 C) exp as in males; enp spiniform, longer than exp1 and with an outer row of three spinules. Leg 6 as an opercular plate armed with two setae or spines. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit.

Species *Remaneicaris oncophora* (Noodt, 1965).

References and synonyms: *Parastenocaris oncophora* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris oncophora* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris oncophora* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris oncophora* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris oncophora* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C138 (M1, slide 6; locus typicus); C138 (M1, slide 1).

Locus typicus: River Cuatro (Córdoba, Argentina).

Male- Length 510 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window (Fig. 48 A) on cephalothorax and 2nd urosomite. Telson without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae (Fig. 51 B). All setae located in distal third. A1 (Fig. 49) 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 50 A)

as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 50 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and four outer spinules. Leg 3 (Fig. 50 C) coxa unarmed; basis with outer seta; enp represented by a bipinated seta; exp 1-segmented, with the apophysis inwardly curved; along the outer margin, with a row of seven spinules on the proximal half and seven stronger spinules along the second half; apophysis is longer than larger, triangular, appearing after a distal depression at the level of the thumb; thumb is long, but shorter than apophysis, ending in a blunt tip. Leg 4 (Fig. 51 A) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules and a PEHZ; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is long, passing the first half of the exp 1, completely hirsute and leaf shaped, with a strong and bipinated distal spinule. Leg 5 triangular and with an inner process; all setae outwardly placed.

Species *Remaneicaris membranacea* (Noodt, 1965).

References and synonyms: *Parastenocaris membranacea* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris membranacea* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris membranacea* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris membranacea* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris membranacea* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C139 (M1, slide 5; locus typicus); C138 (M5, slide 14); C139 (M5, 16).

Locus typicus: River of unknown name in the Pampa, circa of 7 kilometers from the city of San Luiz in the province of San Luiz (Argentina).

Male- Length 480 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window on cephalothorax; 2nd urosomite with a double dorsolateral window. Telson without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae. All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 (Fig. 52 A) as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 (Fig. 52 B) coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-

segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and five outer spinules. Leg 3 (Fig. 53 A) coxa unarmed; basis with outer seta; enp represented by an oval segment with three subdistal spinules; exp 1-segmented, with a hypertrophied, rectangular apophysis inwardly curved in more than 90°; along the outer margin, with a row of seven spinules on the proximal half and twelve spinules along the second half; thumb is very short, strong and almost hidden by the hypertrophied apophysis. Leg 4 (Fig. 53 B) coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; proximally to the enp insertion, with a row of spinules; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size (outermost are bigger than the innermost), one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is short, not reaching the middle of the first exp, of irregular shape, with a cluster of spinules along the inner and concave margin and a distal hyaline membrane. Leg 5 (Fig. 53 D) triangular and with an inner process; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp, leg 5 and genital field.

Length 470- 480 μm . A1 without any special modification, like in the other species previously described. Leg 3 as in the other species of the group. Leg 4 (Fig. 53 D) exp as in males; enp spiniform, longer than exp1 and with an outer row of five spinules; basis with an inner row of spinules. Leg 5 is triangular, with a strong inner process (Fig. 53 E). Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit. Second urosomite with two dorsolateral windows.

Species *Remaneicaris rhizophora* (Noodt, 1965).

References and synonyms: *Parastenocaris rhizophora* Noodt, W. 1965, Beiträge zur Neotropischen Fauna 4: 64-129; *Remaneicaris rhizophora* Jakobi, H. 1972, Crustaceana 22(2): 127-146; *Parastenocaris rhizophora* Rouch, 1986, In: Botosaneanu, L. , Stygofauna Mundi: 321-355; *Parastenocaris rhizophora* Dussart, B. and Defaye, D. 1990, Crustaceana Supplement 16: 1-384; *Remaneicaris rhizophora* Corgosinho, P.H.C. and Martínez Arbizu, P. 2005, Senckenbergiana Biologica 85(2): 147-162.

Observed material: Noodt collection; C137 (M1, slide 9; locus typicus); C137 (M3, slide 13).

Locus typicus: Rio Sierra (La Bolsa), in the mountain between the city of Córdoba and Alta Gracia (Carretera), Córdoba- Argentina.

Male- Length 480 μm (Noodt's measurement). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Dorsal integumental window on cephalotorax; 2nd urosomite with a double dorsolateral window. Telson without ornamentation. Anal operculum smooth and quadratic. Furca with 7 setae. All setae located in distal third. A1 9-segmented and haplocer; armature beginning with proximal segment: 0/5/4/2/5+Ae/1/4/2/9+Ae; last segment with a modified seta. A2 with allobasis; 1-segmented exp with 1 seta, and 1-segmented enp bearing 7 setae. Md, Mx1, and

Mxp armature as in *R. analuizae* Corgosinho and Martínez Arbizu, 2005; Mx2 of the *Remaneicaris* type, with two slender setae on the proximal and three setae on the distal endite. Leg 1 as in the other members of the ingroup 5 (Corgosinho chapter 5), with 1 row of spinules on the inner margin of the enp 1. Leg 2 coxa unarmed; basis without outer seta and with a 1 outer row of spinules, 1 anterior pore and a row of spinules before the insertion of the enp; exp 3-segmented, the first segment being approximately of the same size of the remaining exp; proximally with a strongly developed RVS on the outer margin, with a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without armature and with one spinule located mesially on the outer margin and with a row of distal spinules of unequal size; segment 3 with 3 setae, a distal hyaline frill on the inner corner and one big spinule located mesially, on the outer margin; enp 1-segmented, with a subdistal seta, two distal spinules and a row of outer spinules. Leg 3 as described by Noodt (1965) without enp; apophysis indiscernible. Leg 4 coxa unarmed; basis with outer seta, one pore on the anterior margin and an IBRS; exp 3-segmented, segment 1 almost of the same size of the remaining segments, with an outer spine inserted posteriorly, a proximal row of strongly developed RVS on the outer margin, a row of spinules anterior to the insertion of the outer spine and an inner hyaline frill; segment 2 without setae, with a distal row of spinules of unequal size, one long spinule located mesially at the outer side and a row of spinules along the inner margin; segment 3 with 1 apical and 1 subdistal outer seta, a distal hyaline frill on the inner margin and one big spinule mesially placed on the outer margin; enp is hirsute, with a long distal setae. Leg 5 triangular and with a strong inner process; all setae outwardly placed.

Female: Sexually dimorphic in A1, leg 3, leg 4 enp, leg 5 and genital field.

Length 470- 480 μm . A1 without any special modification, like in the other species previously described. Telson (Fig. 55 B), Leg 1 and 2 (Figs. 54 A and B) as in males. Leg 3 as in the other

species of the group (Fig. 54 C). Leg 4 (Fig. 55 A) exp as in males; enp spiniform, longer than exp1 and with an outer row of three spinules; basis as in *R. membranacea*, with an inner row of spinules. Leg 5 is triangular, with a strong inner process. Genital field with a single mesially located copulatory pore. Gonopore is a transverse slit. Second urosomite with two dorsolateral windows.

Discussion

The genus *Remaneicaris* is a very morphologically diverse group, being composed by organisms from different evolutionary tendencies. Although easily identified by the presence of a number of apomorphies, as well as some plesiomorphies only found, within the family, in this genus, the study of the group raises some problems in what concerns the phylogenetical relationships between the species and groups of species. Thus, sometimes, the decisions can only be made after the observation of the fine ornamentation or of other characters previously undescribed. For example, within the genus, some groups of species (viz. *tridactyla*, *persephone*, *cordobaensis* and *analuzae*) can be well characterized by the shape of the outer row of spinules on the proximal region of the exp 1 of leg 2 and 4 (Corgosinho chapter 5). Following this line of thought, for example, the *analuzae*-group can be only well defined due to the presence of a hyaline structure on the last segment of the A1 of the males, while the *argentina*-group definition was only possible due to the presence of some previously neglected or undescribed characters such as a characteristic hyaline margin on the apophysis, and mainly, due to the presence of a modified spinule near the thumb and the absence of an inner row of spinules on the enp 1 of leg 1 (Corgosinho chapter 5). The same can be seen for a monophylum composed by the groups *persephone* and *cordobaensis*, well supported by the presence of a very controversial character such as the presence of a leg 6 with two seta or spines on the females (Corgosinho chapter 5).

Beyond the neglect of some structures, another important point is the wrong interpretation of some structures that could allow some erroneous interpretation and wrong homologization of characters. In this sense, it is particularly interesting the structure of the males leg 3 in the *argentina*-group. In accordance with Noodt (1965), the thumb is formed by a bifid spine. This could permit some consideration of the possible homology between the thumb seen in the *argentina*-group and the real complex and trifold thumb of *R. tridactyla* and *R. paratridactyla* (Corgosinho *et al.* 2007). However, the mentioned “bifid thumb” of *R. jujuyensis*, *R. argentina* and *R. clandestina* in fact is formed by a single thumb, preceded by a strong spinule, very close to the thumb insertion and that, sometimes, have its own insertion hid by the curvature of the thumb.

Now the genus *Remaneicaris* is faced with another problem. If from one side there are defenders of its condition as on single genus (Martínez Arbizu perss. comm. and Corgosinho chapter 5), there are other researches that believe on its multigeneric condition (Schminke perss. comm.) or even on its polyphyly (Noodt 1965, Noodt 1969). As previously argued (Corgosinho chapter 5), the idea of a multigeneric condition is not out of question and indeed, it is well fundamented. The only problem, however, involves the uncertainty about the future stability of different genera in face of the weak knowledge of the genus in South America. Thus, here we have opted for a more conservative approach, pending a better knowledge of the South America Parastenocarididae fauna.

Thus, considering the species worked here as being members of one single genus, hence, the most basal species within the genus *Remaneicaris* is *R. ignotus*, being well characterized by the presence of some very plesiomorphic characters not even seen before in any other species of this genus. We can mention, for example, the presence of an inner seta on the basis of leg 1 and the presence of dorsal integumental windows on all urosomites (Corgosinho *et al. in press.*). Following *R. ignotus*, the second most “primitive” species is *R. meyerabichi*. In accordance with Noodt (1962),

this species have retained a dorsal “bandförmigen” integumental window on all urosomites. However, our observations revealed that this species have retained the presence of a dorsal integumental window on the 2nd and 5th urosomites only, a character seen again only in *R. palaciosi*. However, *R. meyerabichi* is clearly not closely related to *R. palaciosi*, since it do not shares with the *argentina*-group the complex structure of the leg 3 of males, with the typical hyaline structure on the apophysis and the modified spinule near the thumb. Also, *R. meyerbichi* retains the presence of the inner row of spinules on the enp 1 of leg 1; a character lost at the basis of the *argentina*-group.

Within the *argentina*-group, *R. argentina*, *R. drepanephora*, *R. jujuyensis* and *R. hurdi* are closely related to each other, sharing the presence of a hyaline margin on the modified spinule, near the thumb. The modified spinule does not have any hyaline margin in *R. palaciosi* and *R. clandestina*. An interesting point here is the close relationship between *R. jujuyensis* and *R. hurdi*. Both species seem to share the same morphology of the male's leg 3, with a very long and blade shaped enp, as well as the presence of a strong, curved and pointed thumb before a very characteristic hyaline margin on the apophysis. Unfortunately, due to the absence of the type of *R. hurdi* and due to the bad description provided by Jakobi and Silva (1962), it is really difficult to say if they are the same species or very closed species.

In accordance with Noodt (1965), the species from the group *argentina* should be closely related to *R. icoaraci*. However, this species belong to another monophyletic group within *Remaneicaris*, with whom it shares a very peculiar ornamentation of the basis of male's leg 4, as well as the presence of a modified seta on the last segment of the A1 of the males.

The *tridactyla*-group is represented here by the species *R. hexacantha*, *R. paraguayensis*, *R. remanei* and *R. paraensis*. The definition of this group relies on the presence of a well developed ornamentation on the telson (DRS) and mainly, on the presence of a strong row of spinules on the

ventral margin of the telson, near the insertion of the furca (Corgosinho chapter 5). As mentioned in a previous paper (Corgosinho chapter 5), this is the most basal group within the ingroup 5 and retain the biggest amount of plesiomorphies within it. Thus, the characters used here as synapomorphies, are derived from the observation of ornamentation patterns of the telson. Since these characters are very plastic, appearing also in other species from different monophyletic groups within *Remaneicaris*, this raises some doubts about the strength of them as an autapomorphy for the *tridactyla*-group. However, at the same time, the absence of less inclusive synapomorphies that could support the inclusion of the species that compose the *tridactyla*-group within the groups *cordobaensis* or *persephone*, give us a good support to the acceptance of the telson ornamentations as good characters to define the *tridactyla*-group of species.

Within this group, only *R. hexacantha* have his phylogenetic position not resolved, due to the absence of males. The other species redescribed here, together with *R. juliae*, compose a monophylum within the *tridactyla*-group, defined by the presence of a dorsal row of spinules on the the last urosomite of females. Differently from the other species, in *R. paraensis*, the leg 4 enp of the males is somehow low modified, retaining a resemblance with the enp of the leg 2. In the other species, the same structure is heavily modified, appearing as a well developed, hirsute and leaf shaped enp. Considering the strong ornamentation of males' telson and previous urosomite of *R. remanei* and *R. paraguayensis*, as well as a peculiar modification of the proximal region of the furca on both species, it is reasonable to think about a closer kinship between these species, albeit of the strong difference observed on the leg 3 and 4 of the males.

Beyond *Remaneicaris*, probably there is no other group within the family Parastenocarididae with similar degree of diversity in what concerns the morphology of the leg 3 of males. Unfortunately most of the characters associated to these limbs seem to be plesiomorphic. We can specially mention as a probable plesiomorphic character, the shape of the male's leg three present in

most members of the *analuizae*-groups. In this group this limb is composed by a straight exp, with a short and rounded apophysis and ornamented along the entire outer margin. A similar structure can be seen in *R. meyerabichi* and *R. ignotus*, although in the later species the outer margin do not have any ornamentation. Also, within the *persephone* and *tridactyla* groups, there is no character linked to the leg 3 of males that could be used to define any of these groups. In this sense, it is really helpful the characteristic inner process present in the exp of the leg 3 of the species belonging to the *cordobaensis*-group. This character can not be seen in other groups within *Remaneicaris*, being therefore interpreted by Corgosinho (chapter 5), as an autapomorphy for the *cordobaensis*-group.

In what concerns the morphology of the leg 3 of the males of the *cordobaensis*-group, Noodt (1965) described the apophysis as a hyaline process. However, our observations revealed a chitinized apophysis, although not so strongly chitinized as the previous exp.

Within the *cordobaensis*-group, *R. sierrae* is a sister taxon of a group formed by *R. cordobaensis* and *R. ciliata*, with whom it shares the absence of the developed row of spinules near the insertion of male's leg 4 enp, and the absence of a PEHZ. Within this group, *R. sanctiludovici* is the most basal species, retaining, as a plesiomorphy, the PEHZ and the developed row of spinules near the enp of the leg 4 of males. In accordance with Noodt (1965), *R. sierrae* is closely related with all these species, plus *R. pluto*. However, in accordance with Corgosinho (chapter 5) this later species belongs to the *persephone*- group, with whom it shares the presence of the double dorsolateral integumental window on the 2nd urosomite of males and double genital somite of females, and a well developed enp on females leg 4, that is bigger than the exp 1. Furthermore, Noodt (1965) mentioned that *R. sierrae* is closer related to *R. cordobaensis*. However, later, in the same paper, he mentioned that *R. cordobaensis* and *R. ciliata* should be closer. Thus, it is not clear, however, which of these possibilities is the most probable for this author, albeit of his consideration about the almost equal ornamentation of the appendices of *R. cordobaensis* and *R. ciliata*. In

accordance with him, due to this strong similarity, both species can only be separated on the basis of the fine ornamentation of legs 2 and 4 of males, as well as due to the dorsal ornamentation of the furca of males of *R. ciliata*. We agree with a closer relationship between *R. cordobaensis* and *R. ciliata*, supported by the presence of an inner row of spinules on the basis of the leg 3 of males, prior to the insertion of the enp as a synapomorphy (Corgosinho chapter 5). Additional differences between both species can be seen also in the male's leg 3. Here we can see that while in *R. ciliata* the thumb is “naked”, in *R. cordobaensis* it has an inner hyaline margin, existing also an additional difference in what concerns the shape of the apophysis.

The proposition of Noodt (1965) about the possible position of *R. sanctiludovici* and *R. pluto* within *Remaneicaris* is particularly intriguing. In accordance with this author, these species should be placed between the groups *cordobaensis* and *persephone*. Excluding the possible close relationship of *R. argentina* with these species, as proposed by Noodt (1965), even after his initial proposition (see Noodt 1965, page 105 and 104), it remains interesting how his ideas approximate from ours. However, they are completely detached from any phylogenetical meaning, since an intermediate step between both groups is impossible on the light of any phylogenetical reasoning. Thus, although not explicitly detailed by this author which characters should unite both groups around *R. pluto* and *R. sanctiludovici*, it is curious to see that he found a closer relationship between the groups *persephone* and *cordobaensis* (as proposed by Corgosinho (chapter 5).

Considering the *persephone*-group, the most derived species are *R. membranacea* and *R. rhizophora*. The absence of a leg 6 armed with spines or setae, together with the presence of a row of spinules on the inner margin of the female's leg 4 and an apophysis inwardly curved in more than 90°, are good synapomorphies that support this kinship. In accordance with Noodt (1965), *R. oncophora* should be also considered a species within this monophylum, being closely related to *R. rhizophora*. However, our data do not support this assumption, being *R. oncophora* closely related

with *R. pluto*, with whom it shares the presence of a depression on males leg 3, near the apophysis. Finally, the proximity of *R. hecate* and *R. persephone* is well justified on the basis of the general morphology of the leg 3 of males (plesiomorphy?) and due to the presence of a blade shaped emp on the leg 4 of the females.

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We would like to thank the Deutscher Akademischer Austausch Dienst “DAAD” the Fundação de Amparo a Pesquisa do Estado do Amazonas and the Forschungsinstitut Senckenberg for the financial support of the senior author. We are in debt with the DZMB- Senckenberg Forschungsinstitut and the Instituto Nacional de Pesquisas da Amazônia for the logistic support during this work. Prof. Dr. Schminke (University of Oldenburg) for discussions on parastenocaridid phylogeny and Dr. Thomas Glatzel (University of Oldenburg) for allowing us to study his personal collection of Parastenocarididae. We are in debt to Dr. Frank Ferrari, Dr. Chad Walter and Dr. Daniele Defaye for the loan of some type species used during this study. This study would not have been possible without the study of Noodt’s type material. We are especially in debt to Dr. Ahmed Ahnert who curated Noodt’s material after he passed away and put it at our disposal for the present study.

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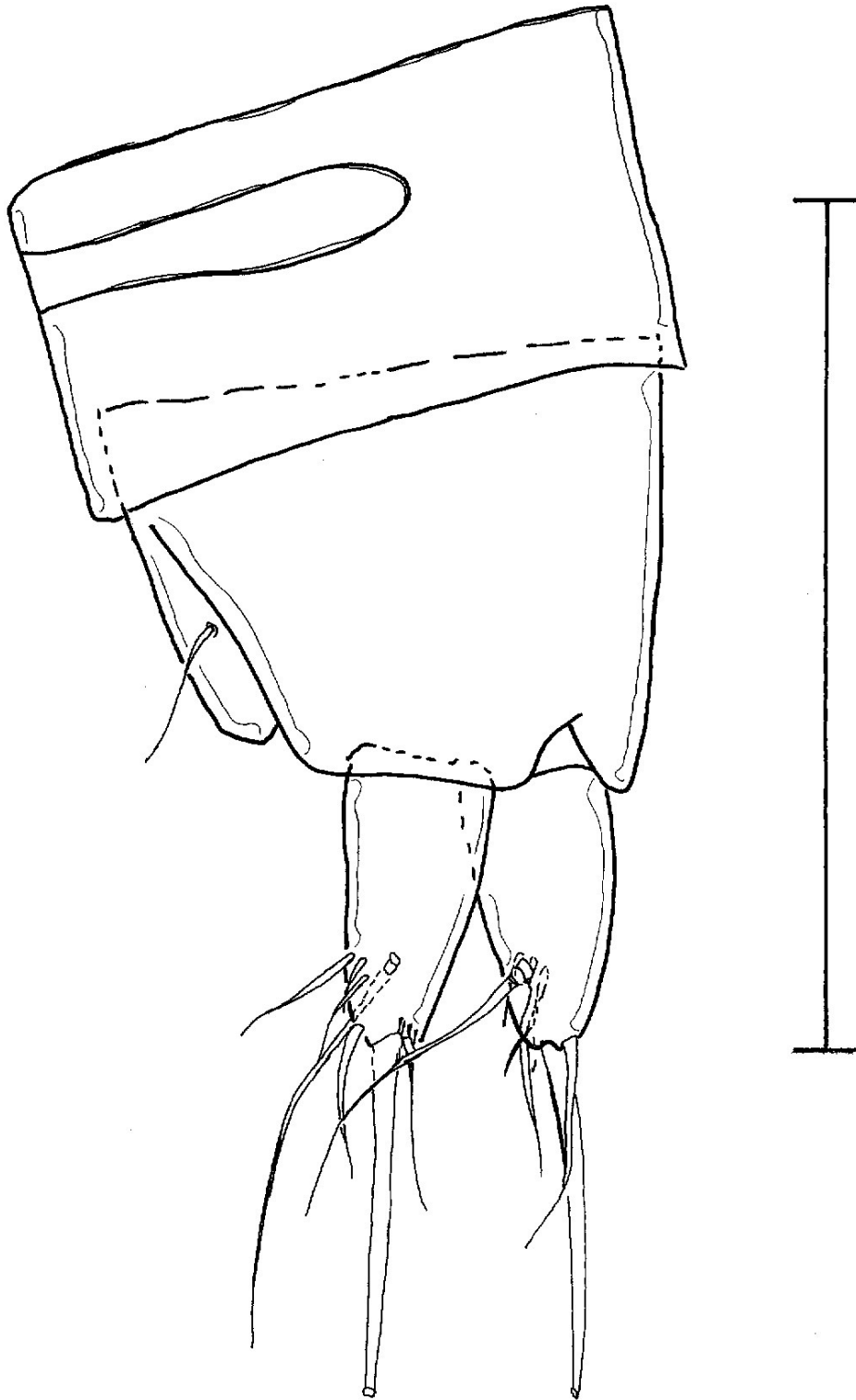


Figure 01- *Remaneicaris meyerabichi* (Noodt, 1962); male, telson. Scale bar= 100 μ m.

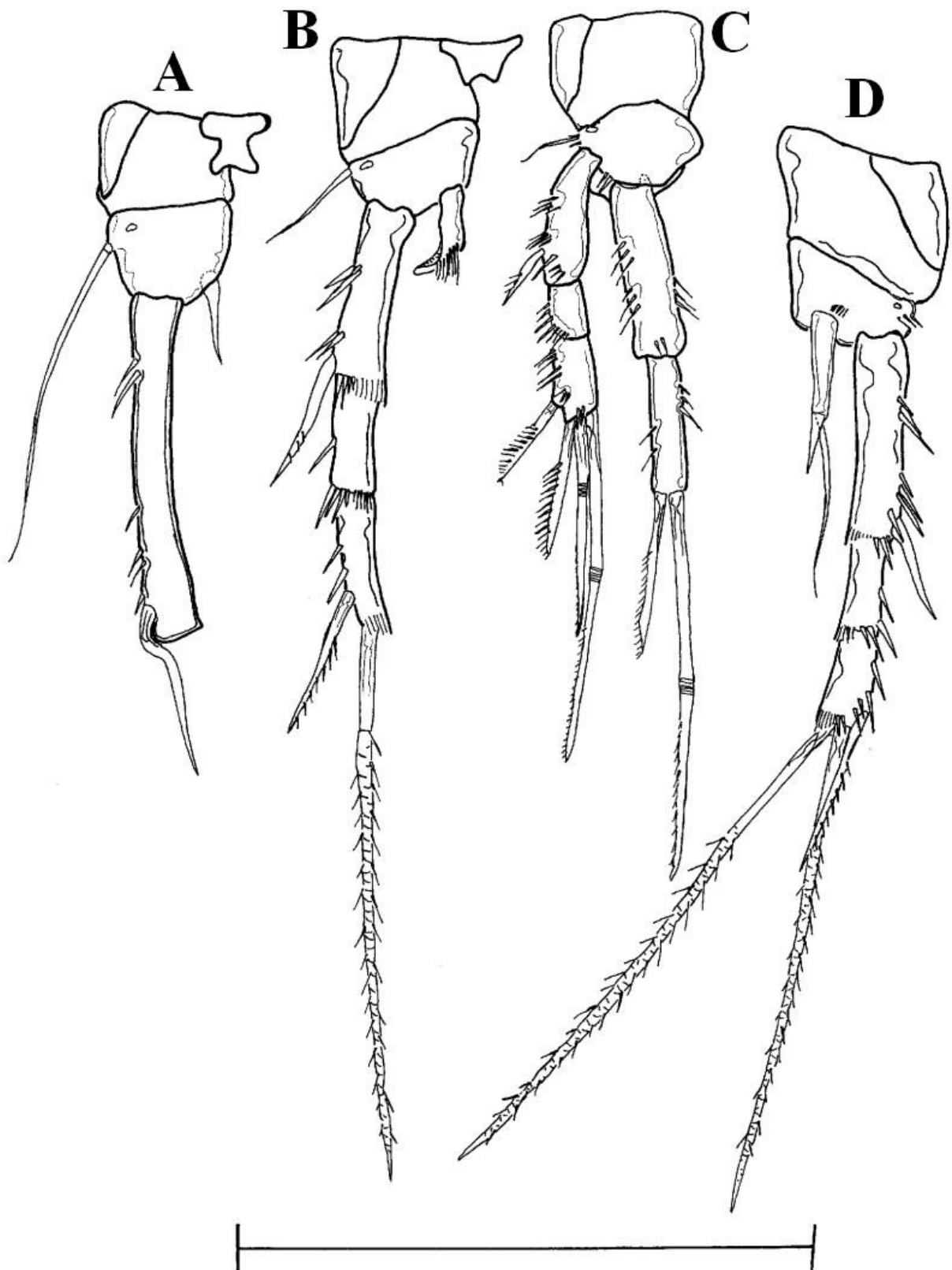


Figure 02- *R. meyerabichi* (Noodt, 1962); male. A, leg 3; B, leg 4; C, leg 1 and D, leg 2. Scale bar= 50 μ m.

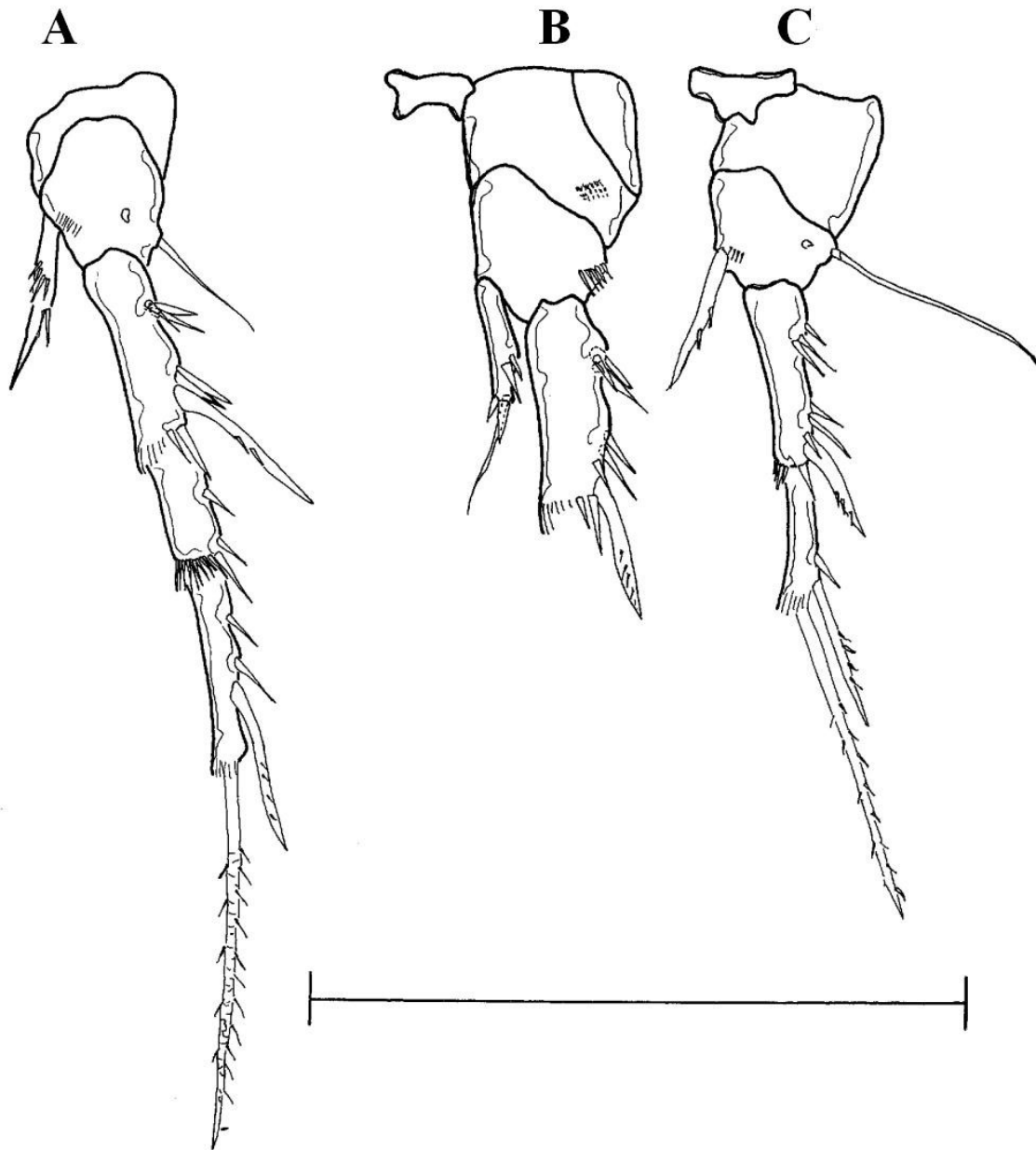


Figure 03- *R. meyerabichi* (Noodt, 1962); female. A, leg 4; B, leg 2 and C, leg 3. Scale bar= 50 μ m.

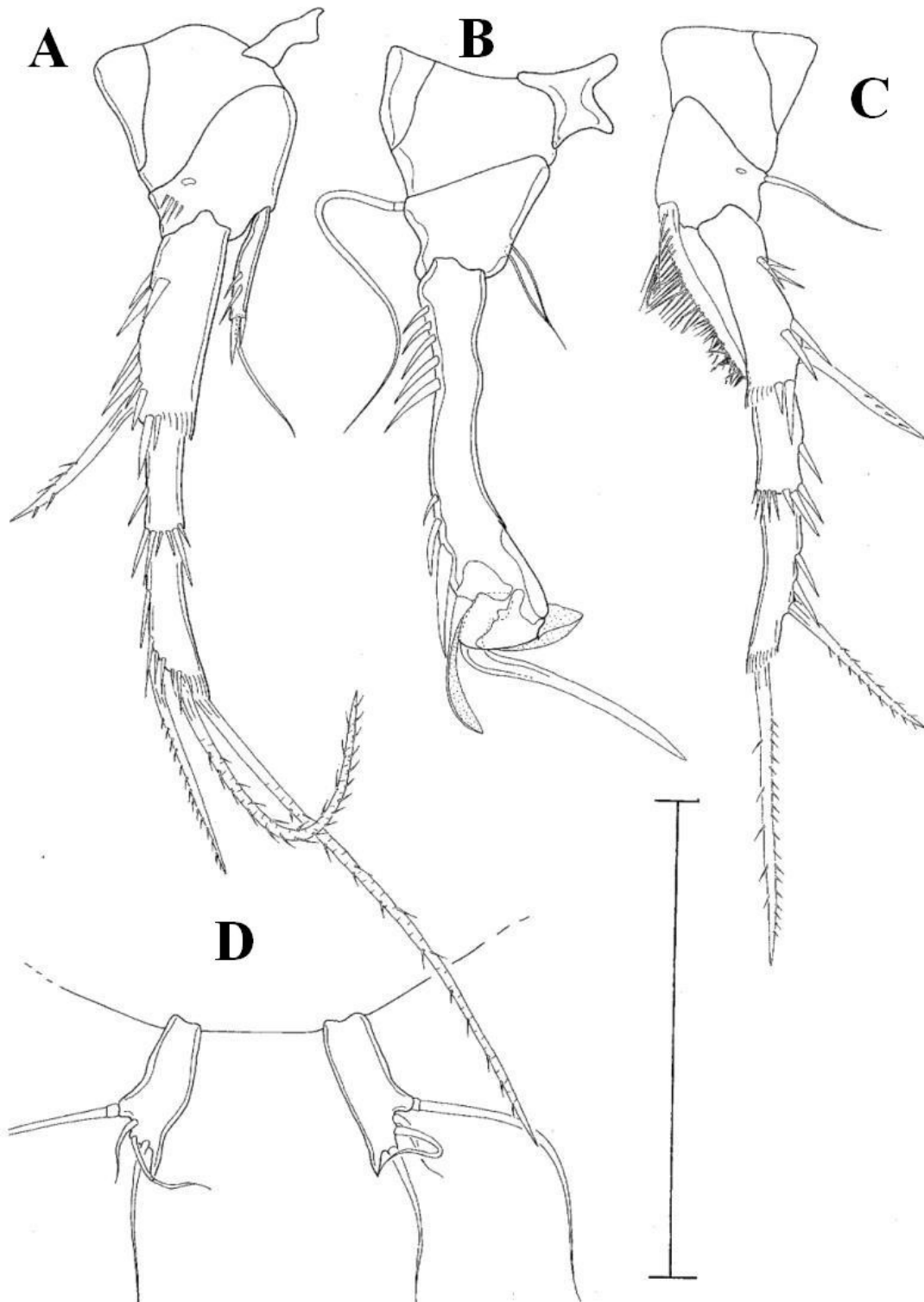


Figure 04- *Remaneicaris argentina* (Noodt, 1965), male. A, leg 2; B, leg 3; C, leg 4 and D, leg 5. Scale bar= 50 μ m.

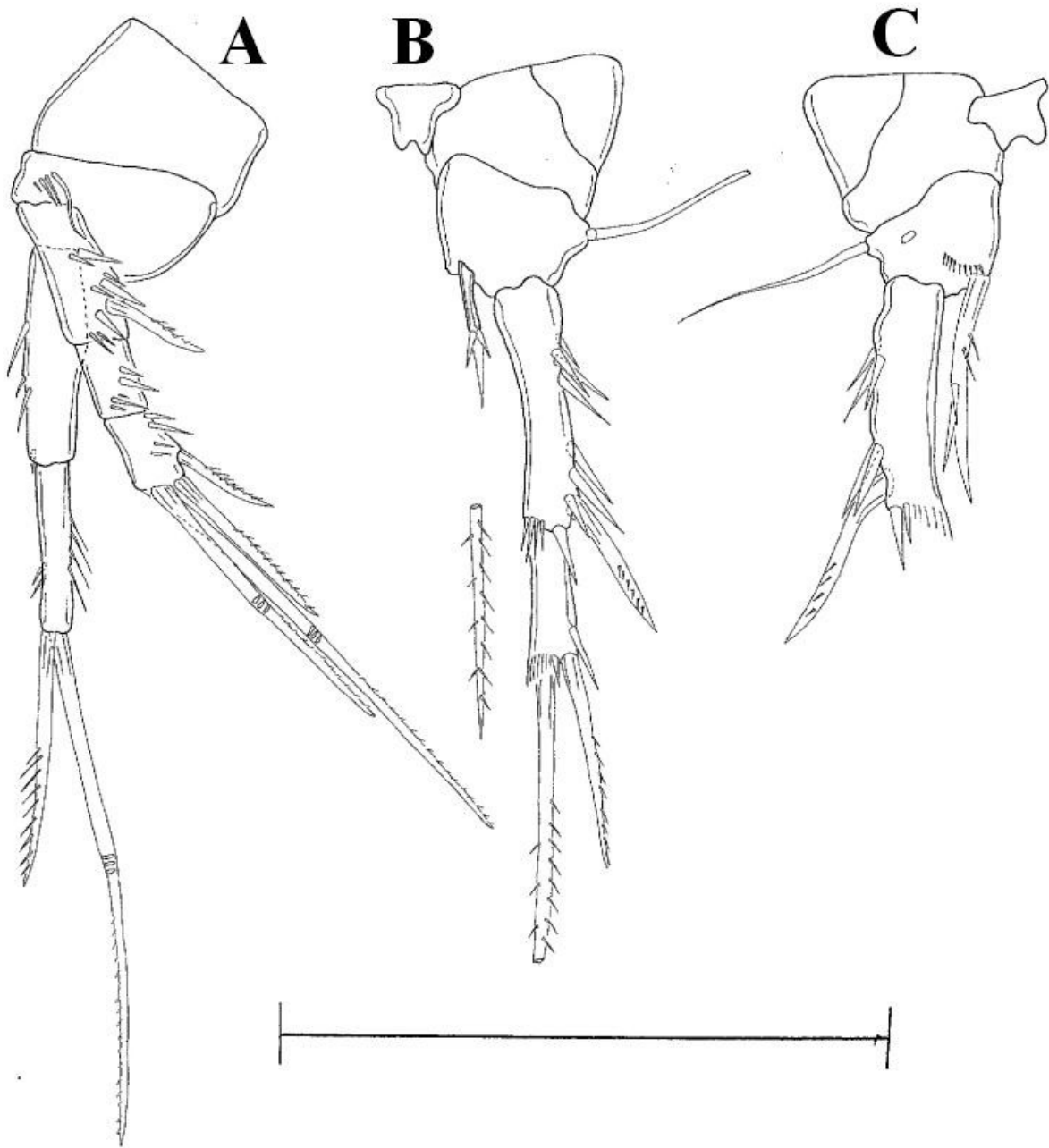


Figure 05- *R. argentina* (Noodt, 1965), female. A, leg 1; B, leg 3; C, leg 4. Scale bar= 50 μ m.

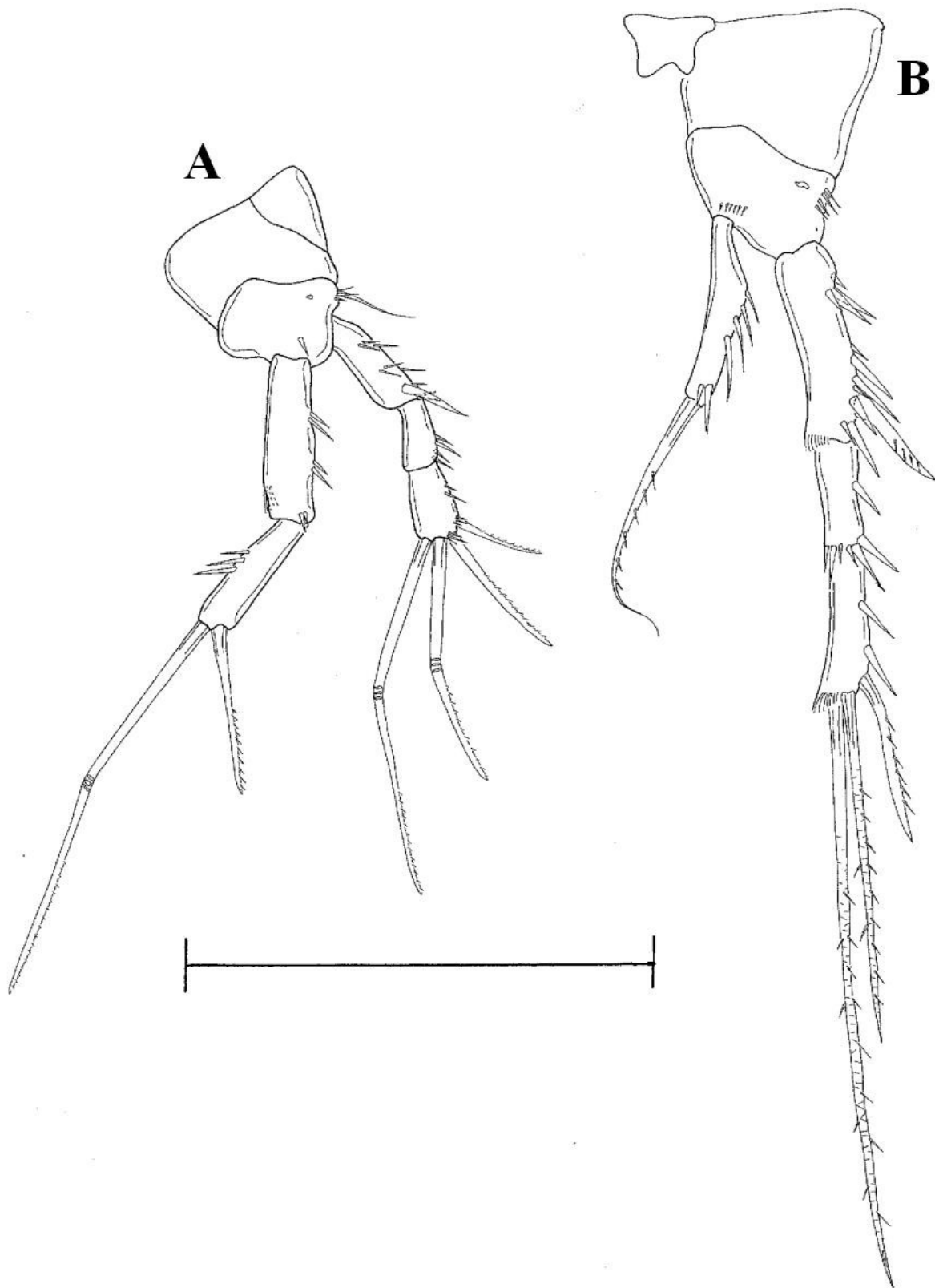


Figure 06- *Remaneicaris jujuyensis* (Noodt, 1965), male. A, leg 1; B, leg 2. Scale bar= 50 μ m..

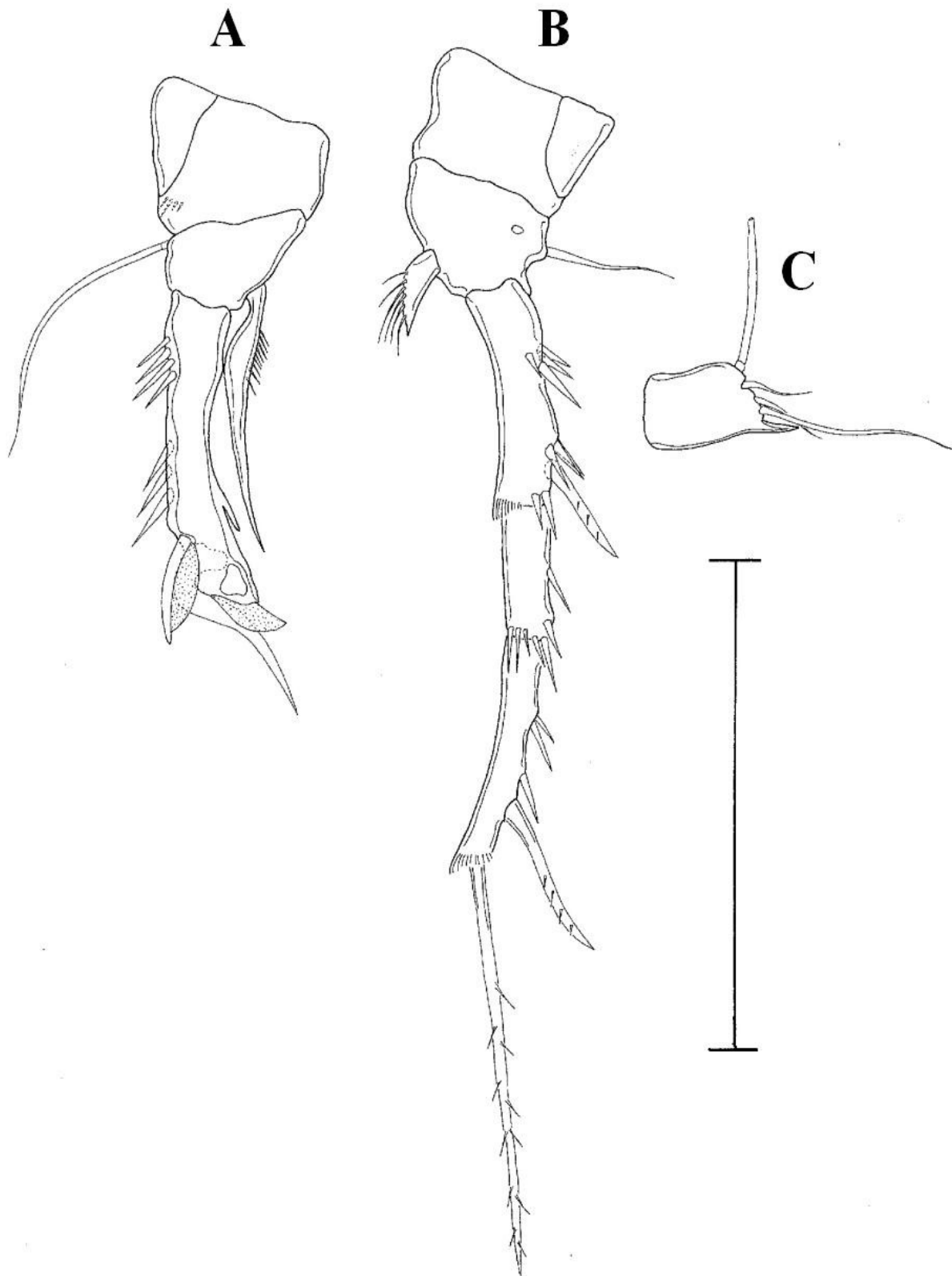


Figure 07- *Remaneicaris jujyensis* (Noodt, 1965), male. A, leg 3, B, leg 4, C, leg 5. Scale bar= 50 μ m.

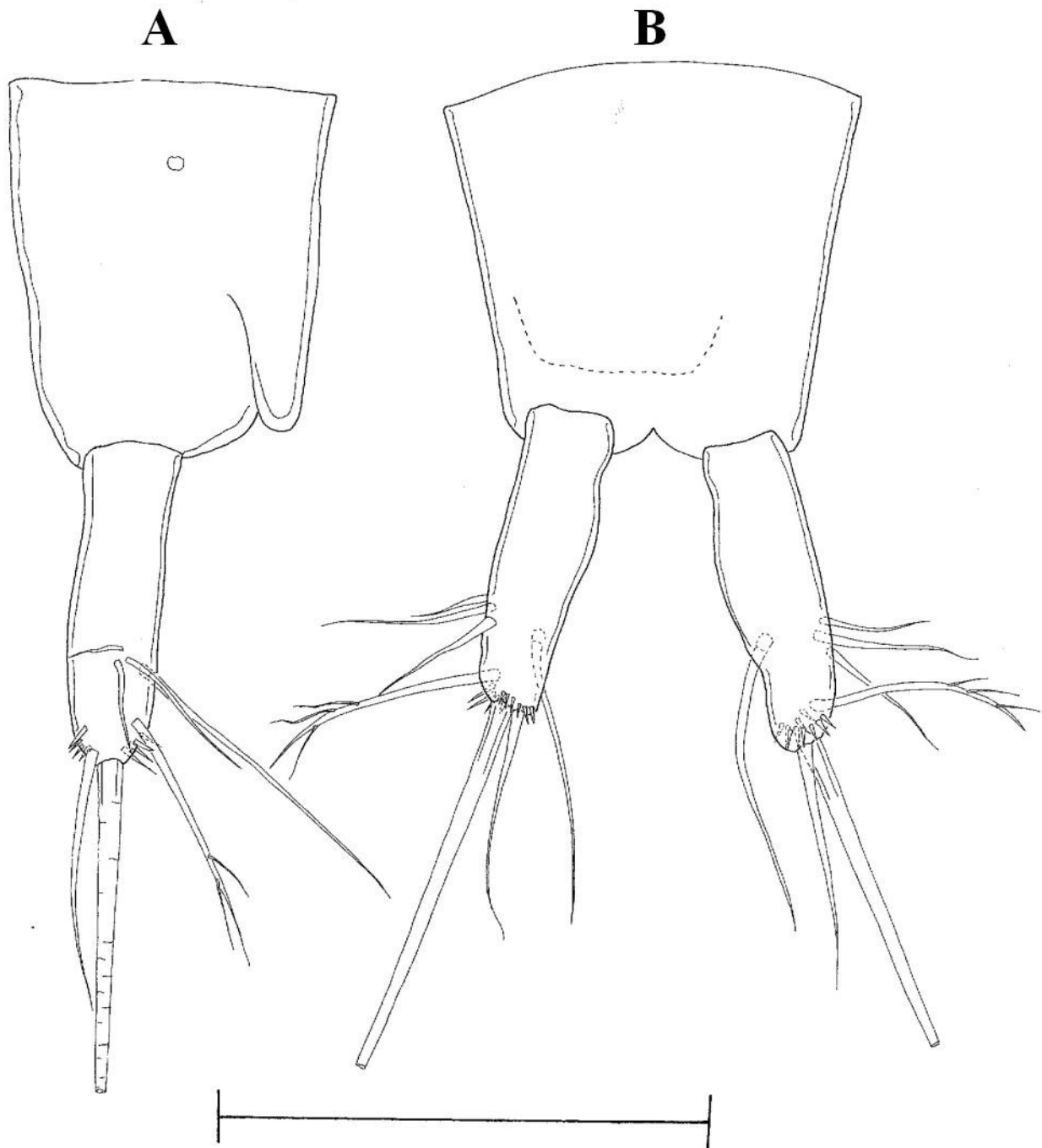


Figure 08- *Remaneicaris drepanephora* (Kiefer, 1967), male. A, telson lateral view; B, telson ventral view. Scale bar= 50 μ m.

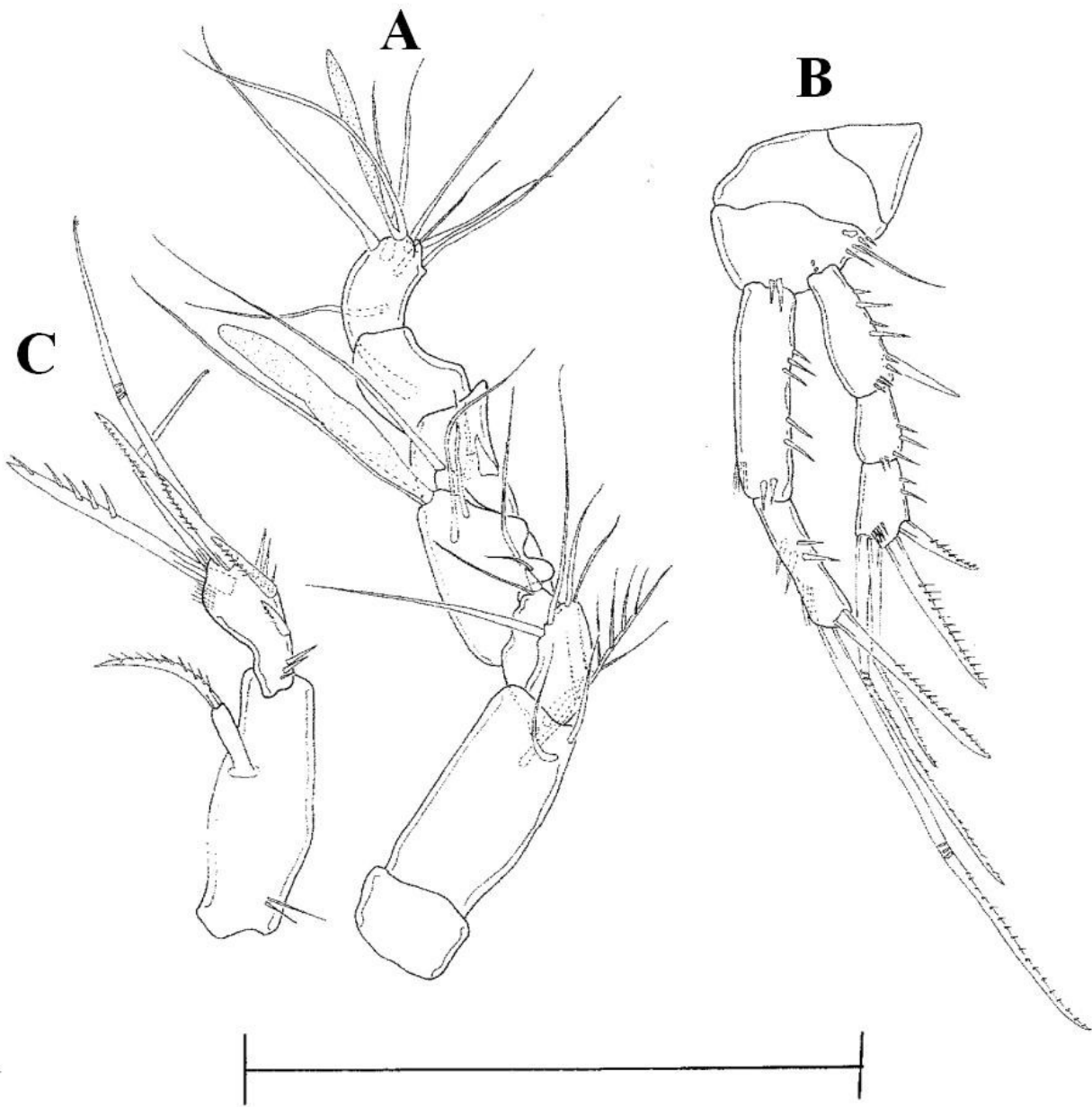


Figure 09- *Remaneicaris drepanephora* (Kiefer, 1967), male. A, antennule; B, antenna; C, leg 1. Scale bar= 50 μ m.

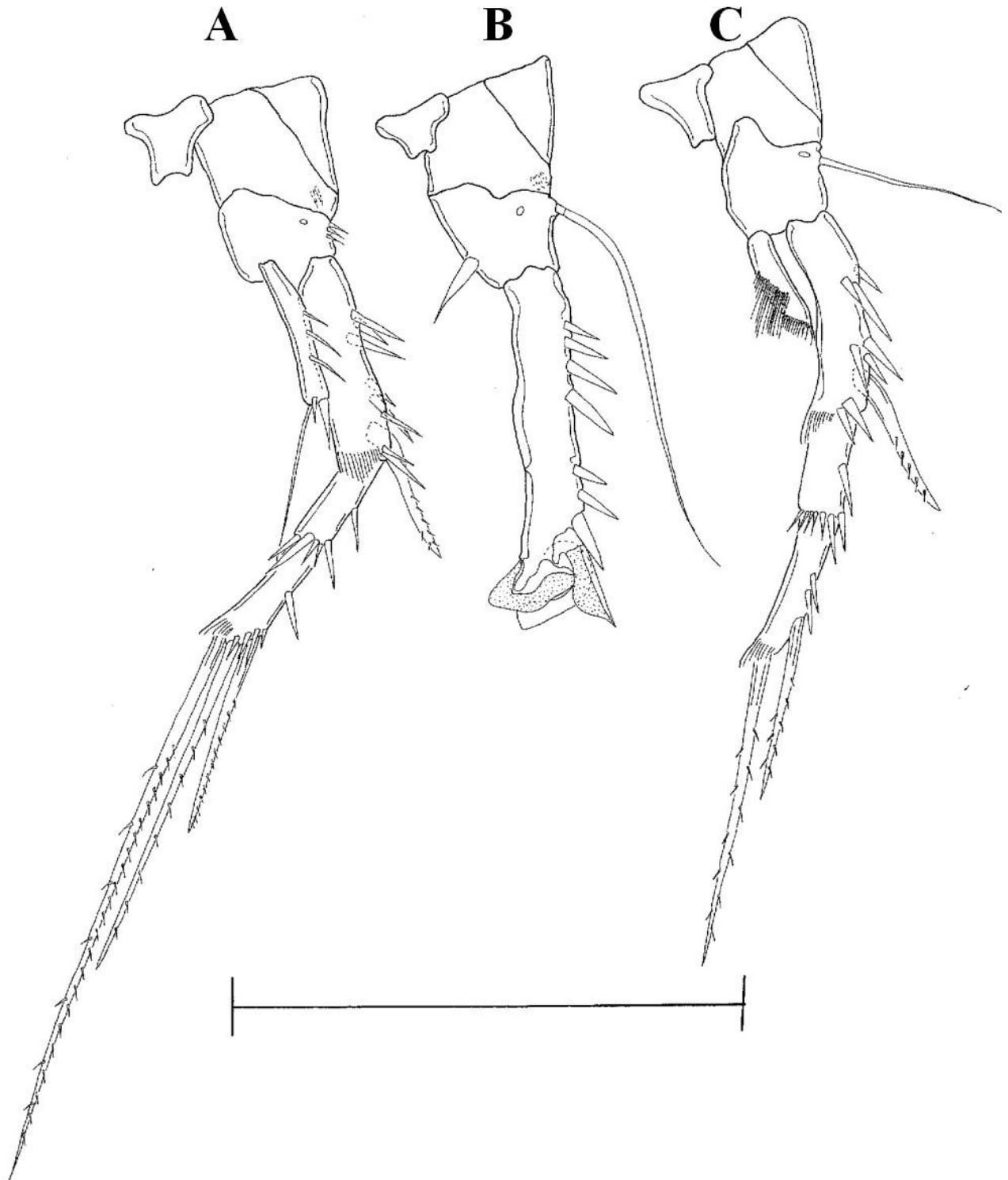


Figure 10- *Remaneicaris drepanephora* (Kiefer, 1967), male. A, leg 2; B, leg 3; D, leg 4. Scale bar= 50 μ m.

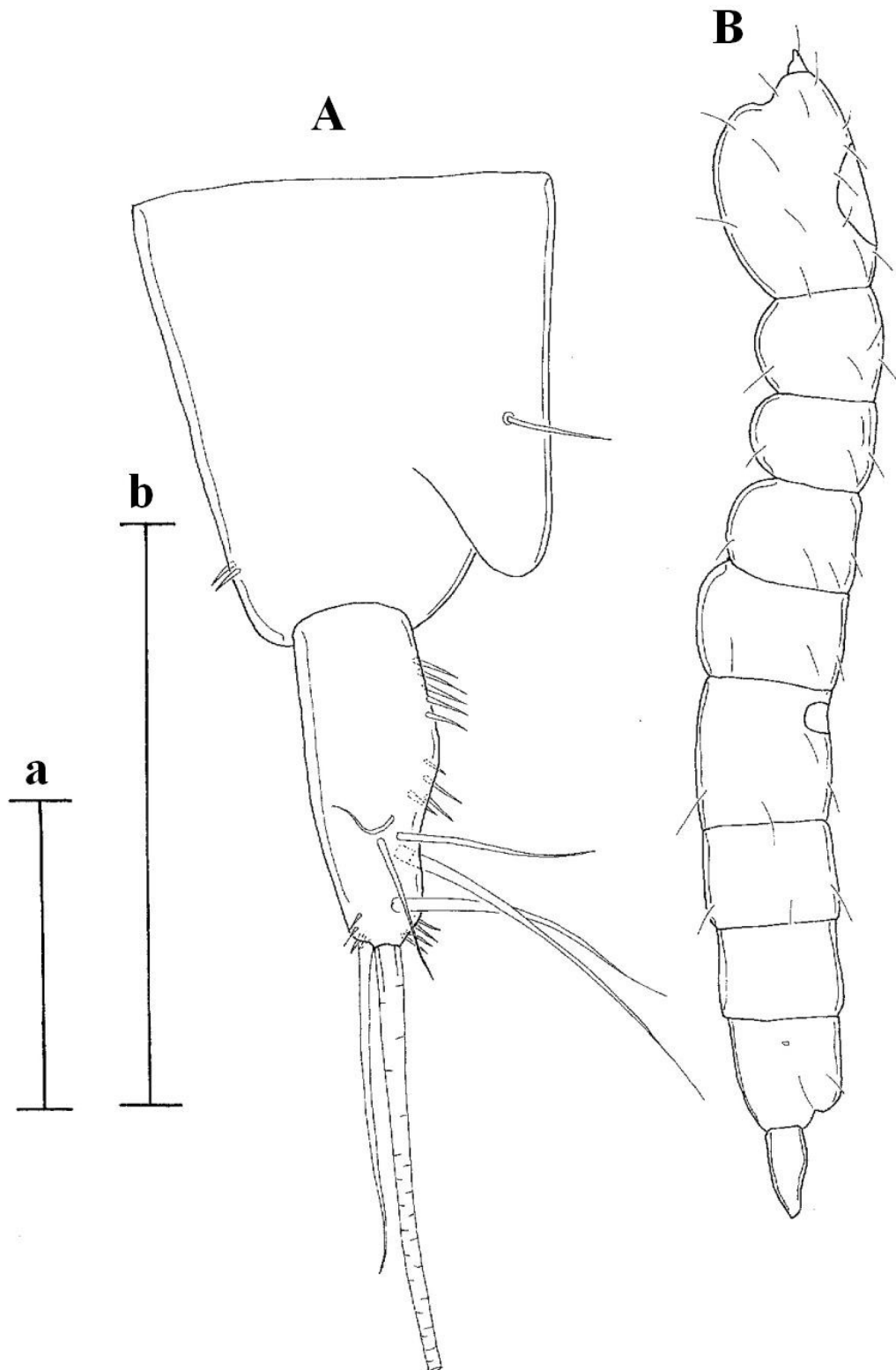


Figure 11-*Remaneicaris drepanephora* (Kiefer, 1967), female. A, telson lateral view; Scale bar b= 50 μ m; B, habitus lateral; Scale bar a= 100 μ m.

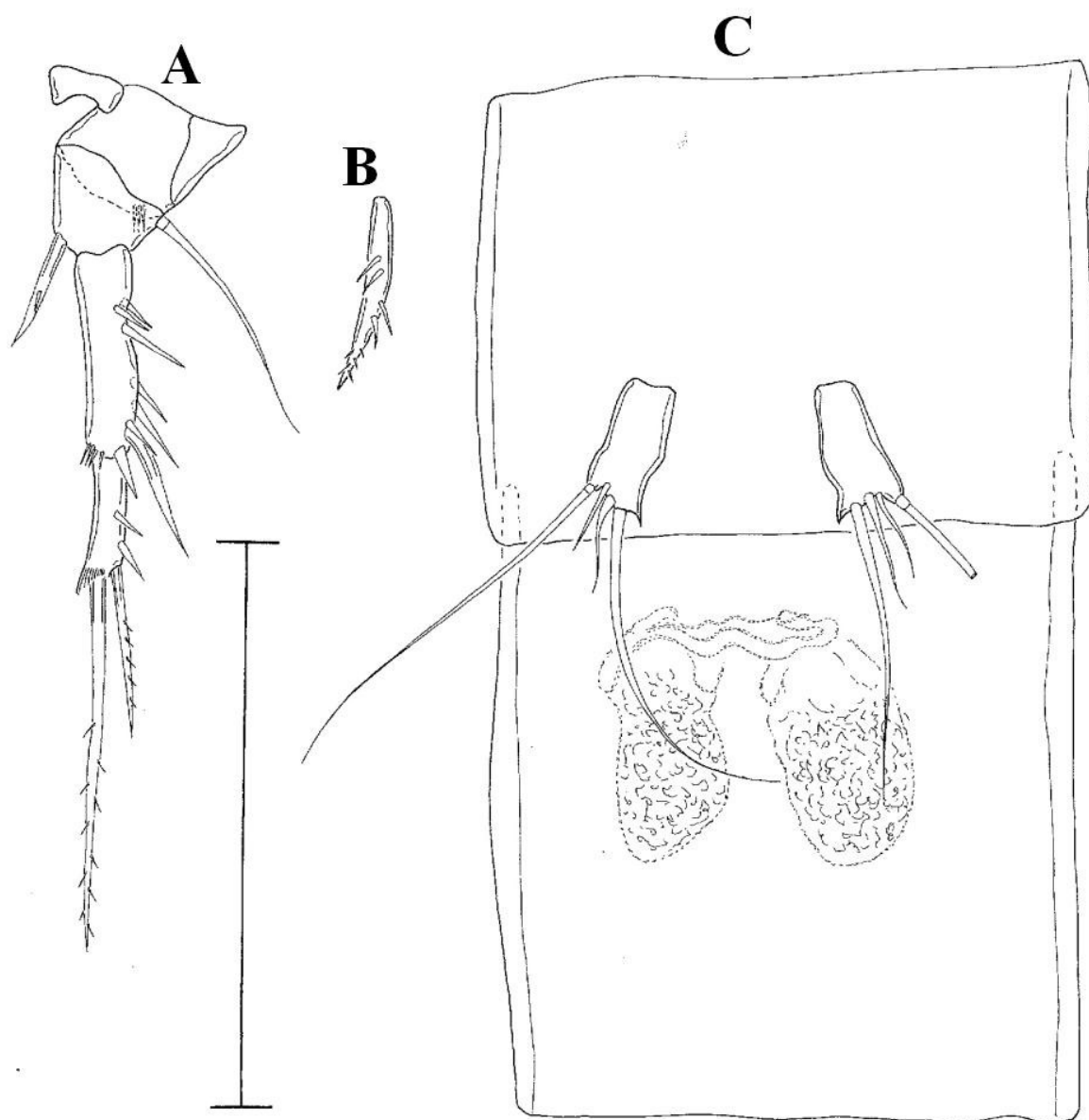


Figure 12- *Remaneicaris drepanephora* (Kiefer, 1967), female. A, leg 3; B, end of leg 4; C, leg 5 and genital somite. Scale bar= 50 μ m.

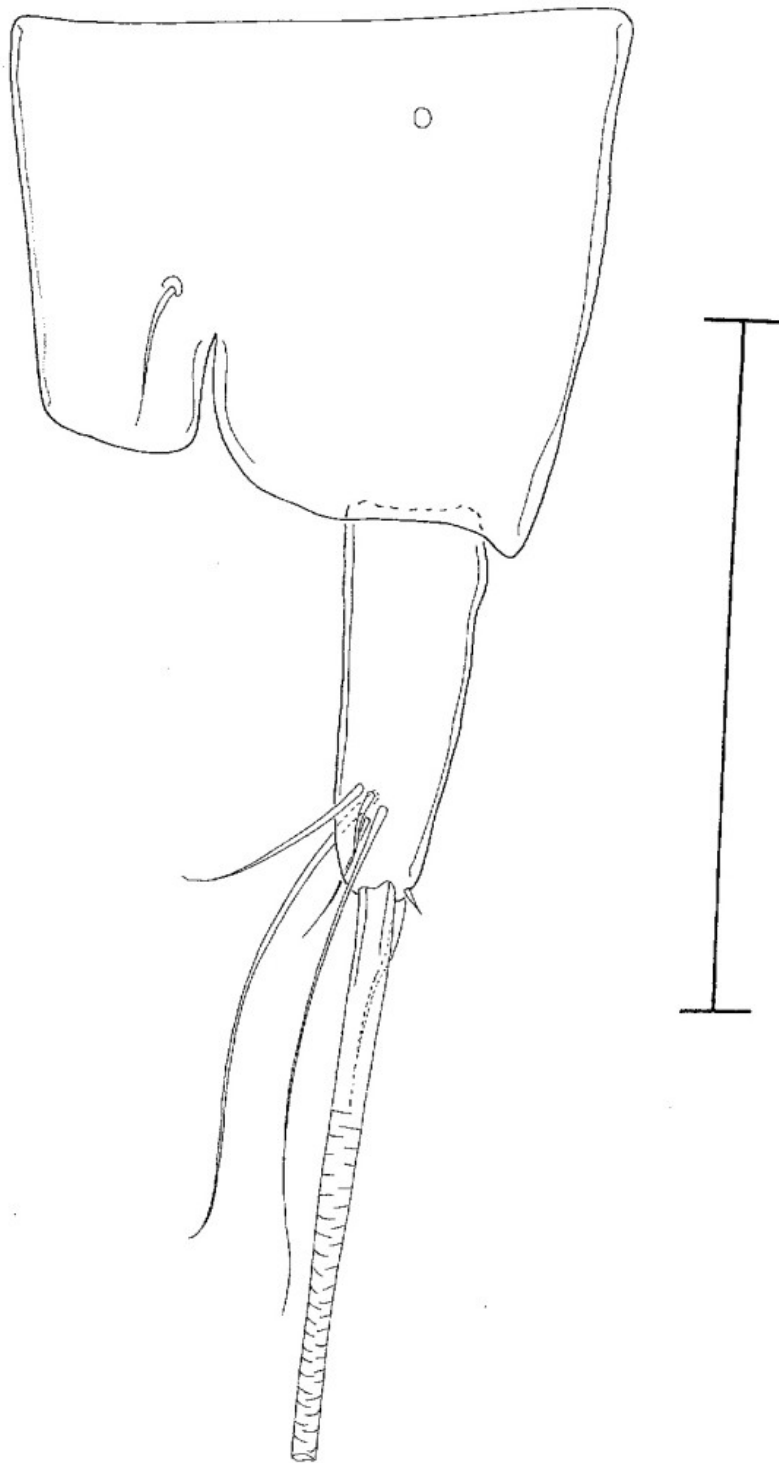


Figure 13- *Remaneicaris palaciosi* (Noodt, 1962), male. telson, lateral view. Scale bar= 50 μ m.

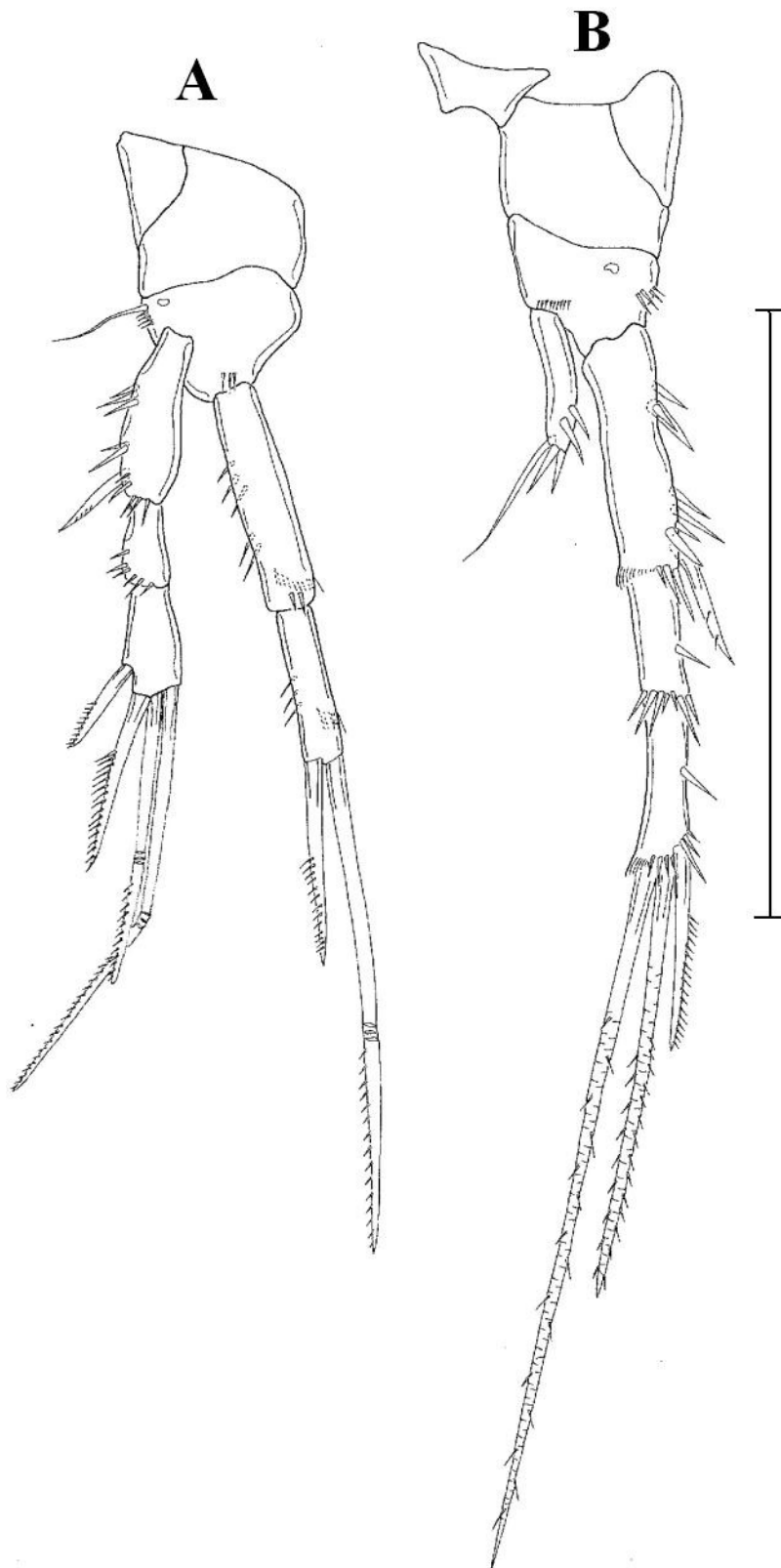


Figure 14- *Remaneicaris palaciosi* (Noodt, 1962), male. A, leg 1; B, leg 2. Scale bar= 50 μ m.

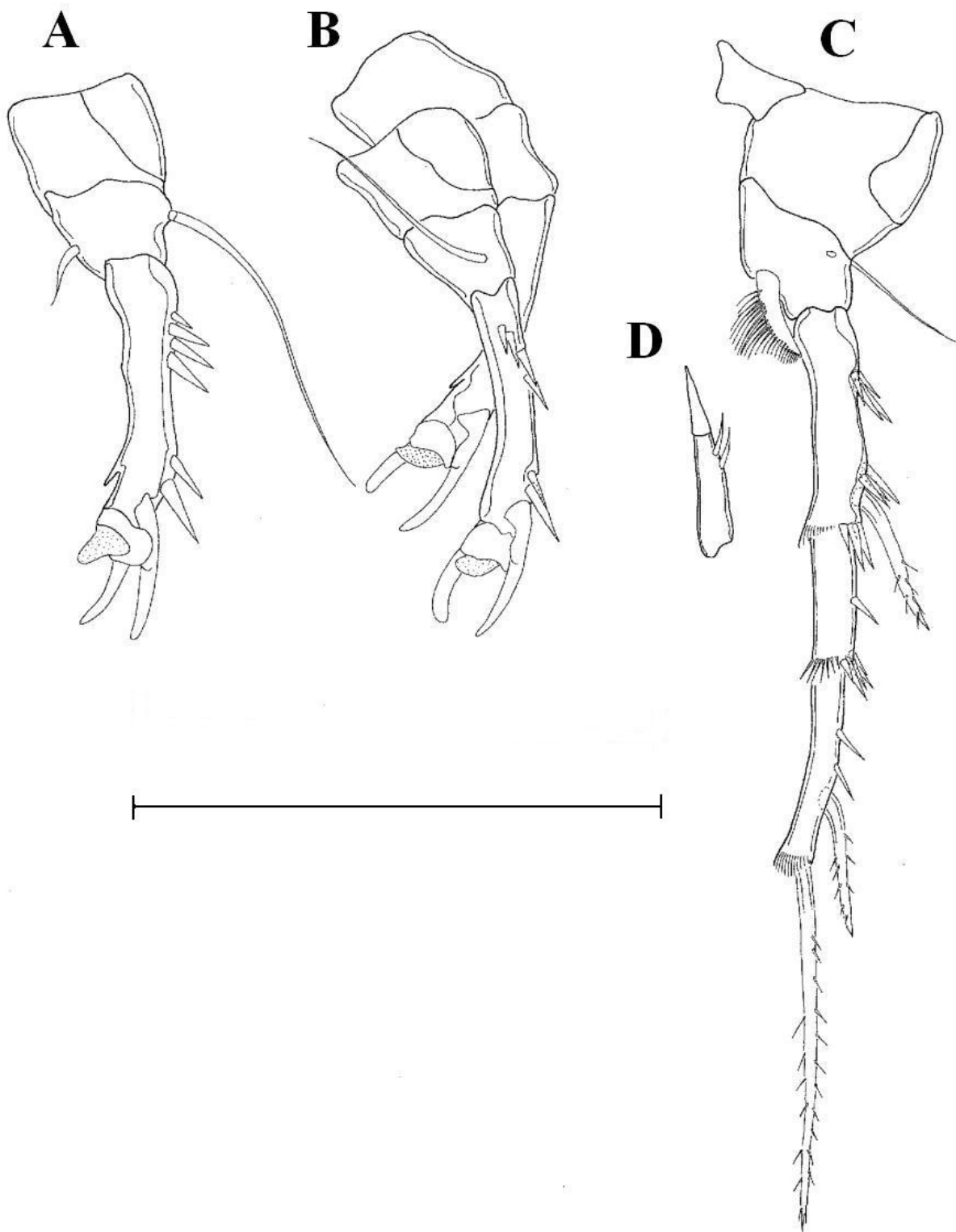


Figure 15- *Remaneicaris palaciosi* (Noodt, 1962), male. A, leg 3, ventral view; B, leg 3, lateral view; C, leg 4 and D, end of female's leg 4. Scale bar= 50 μ m.

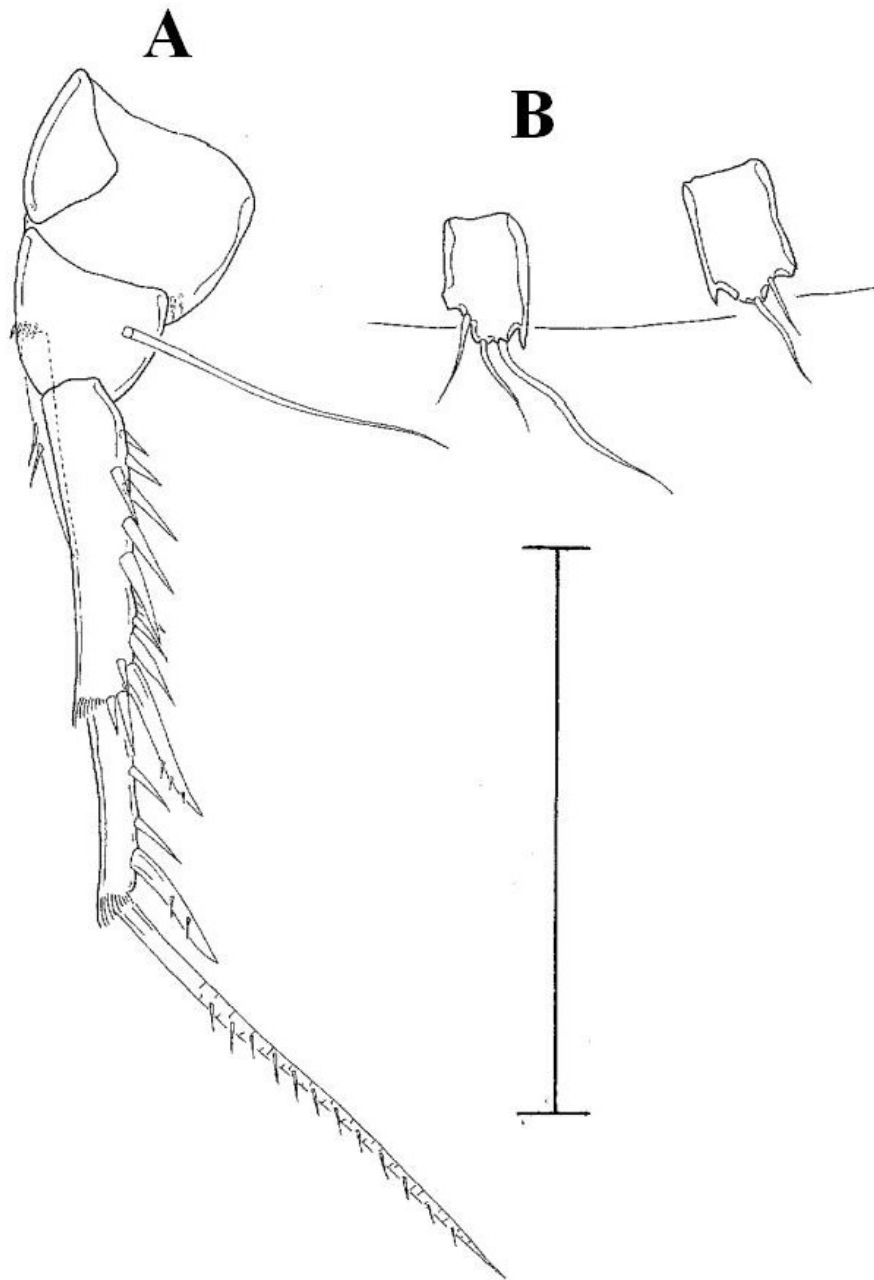


Figure 16- *Remaneicaris palaciosi* (Noodt, 1962). A, leg 3 of female; B, leg 5 of male (damaged). Scale bar= 50 μ m.

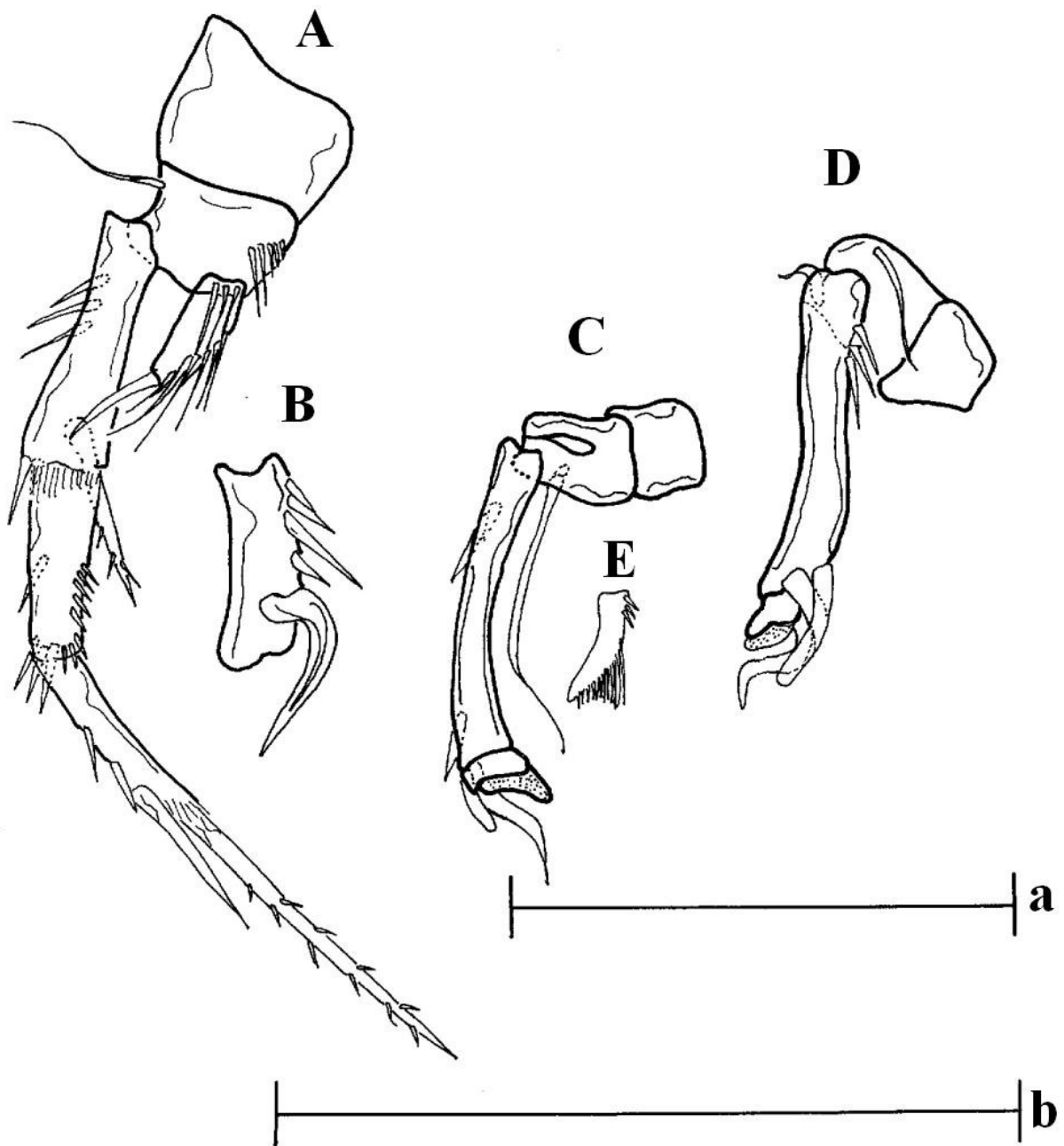


Figure 17- *Remaneicaris icoaraci* (Noodt, 1963), male. A, leg 4; B, apophysis and thumb of leg 3; Scale bar b= 50 μ m. *Remaneicaris clandestina* (Noodt, 1963), male. C, leg 3, ventral view; D, leg 3, lateral view; E, end of leg 4. Scale bar a= 50 μ m.

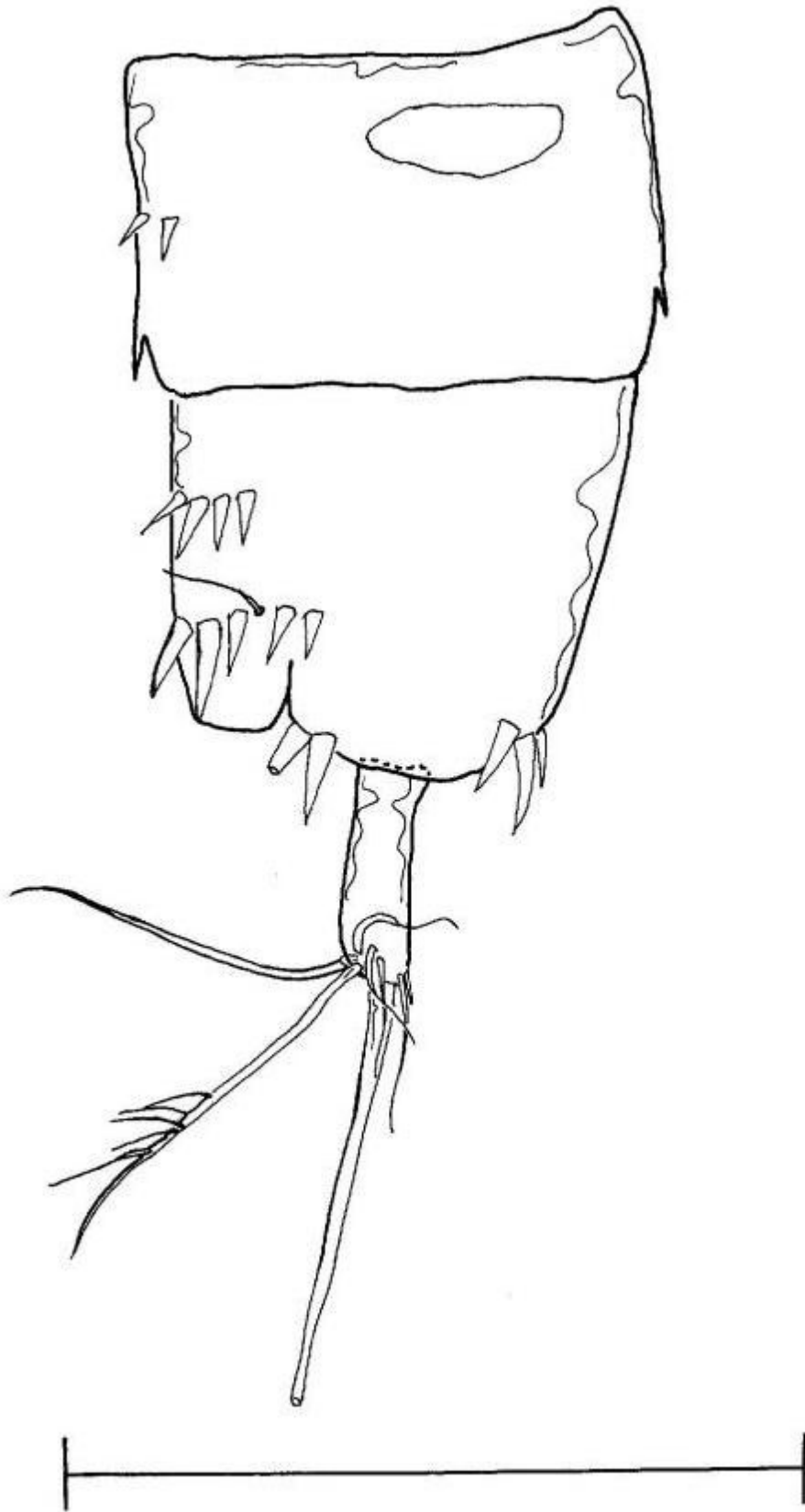


Figure 18- *Remaneicaris remanei* (Noodt, 1963). telson of male in a lateral view. Scale bar= 50 μ m.

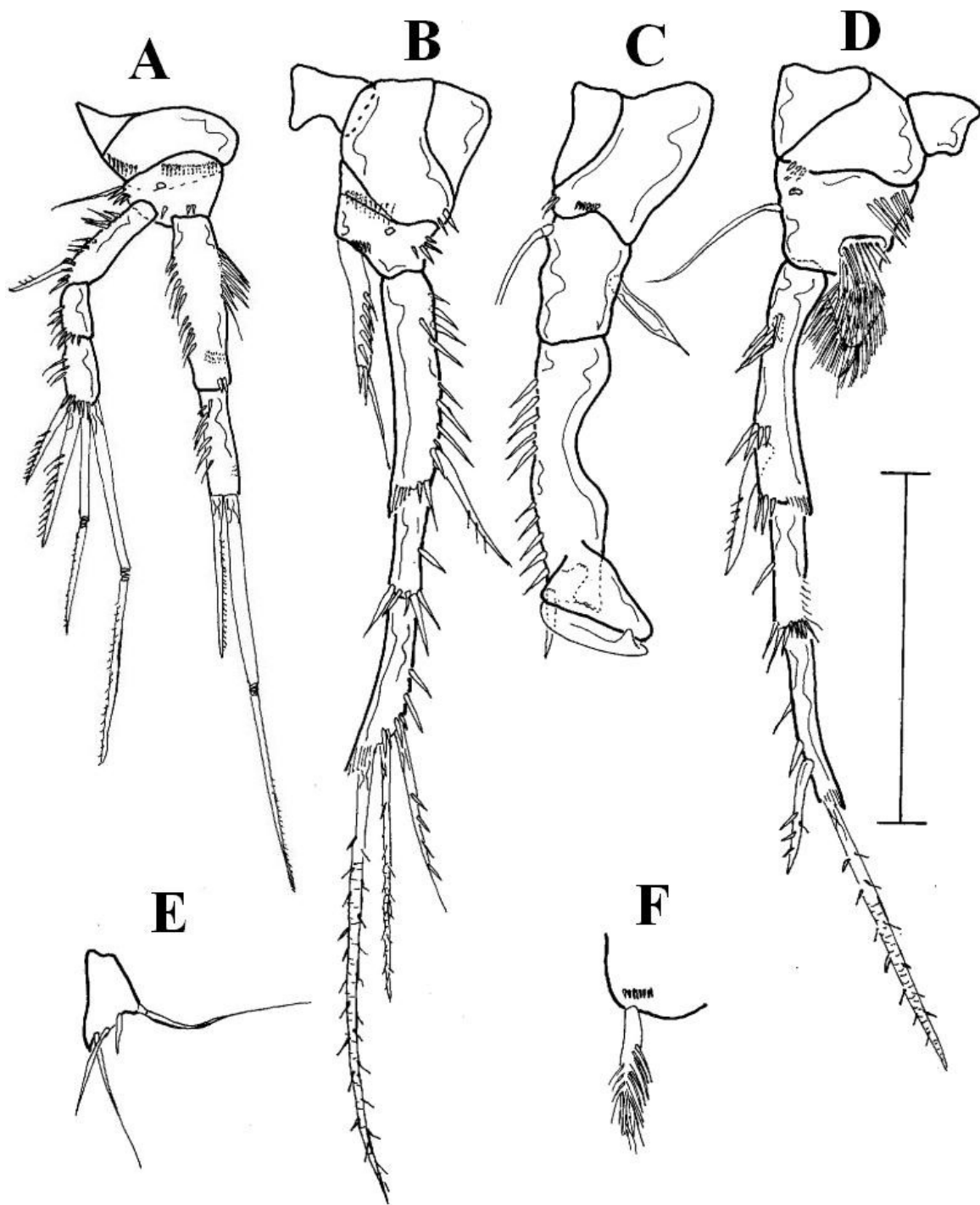


Figure 19- *Remaneicaris remanei* (Noodt, 1963), male. A, leg 1, B, leg 2, C, leg 3; D, leg 4; E, leg 5; F, end of female's leg 4. Scale bar= 50 μ m.

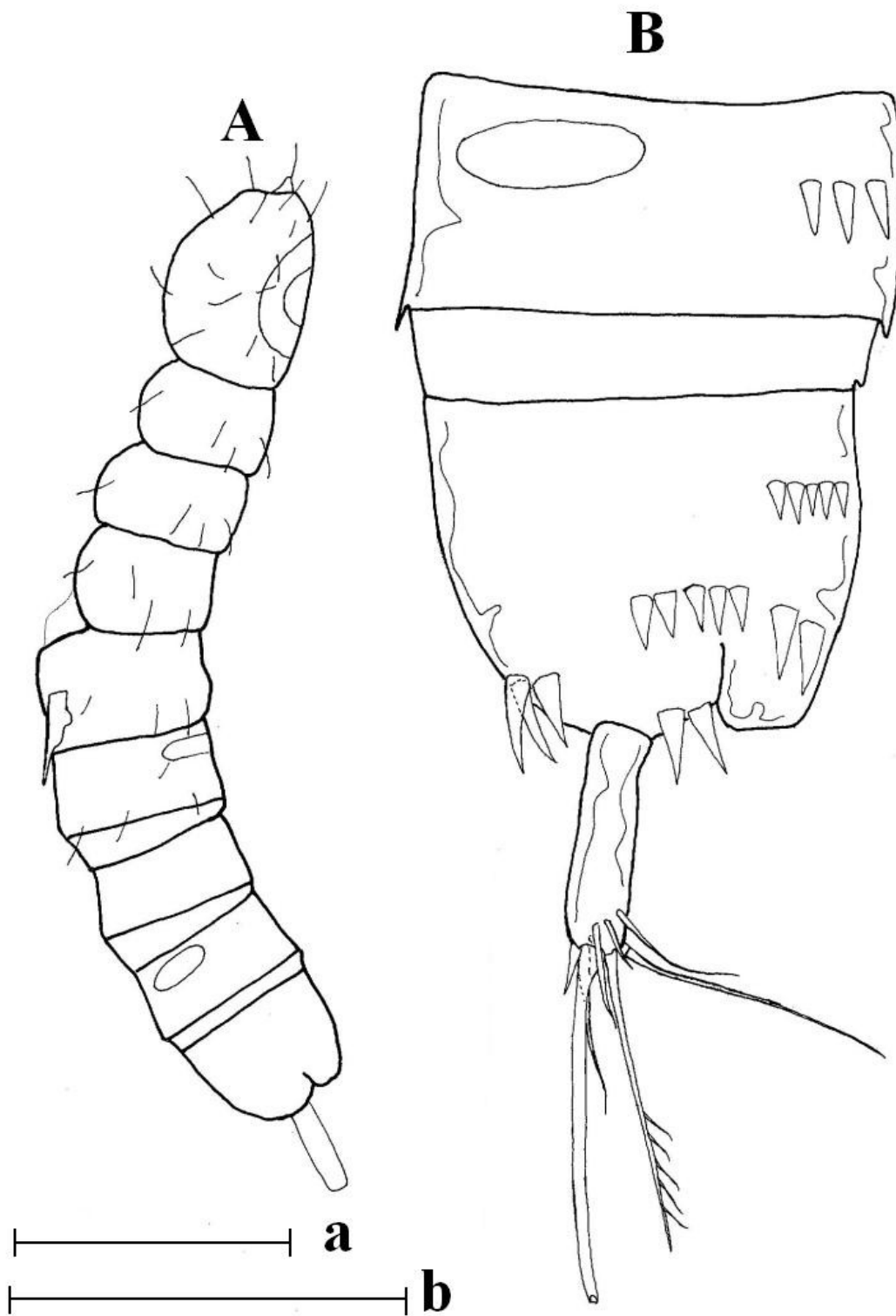


Figure 20- *Remaneicaris paraguayensis* (Noodt, 1963), male. A, habitus lateral; Scale bar a= 50 μ m. B, telson and last urosomite in a lateral view; Scale bar b= 50 μ m. .

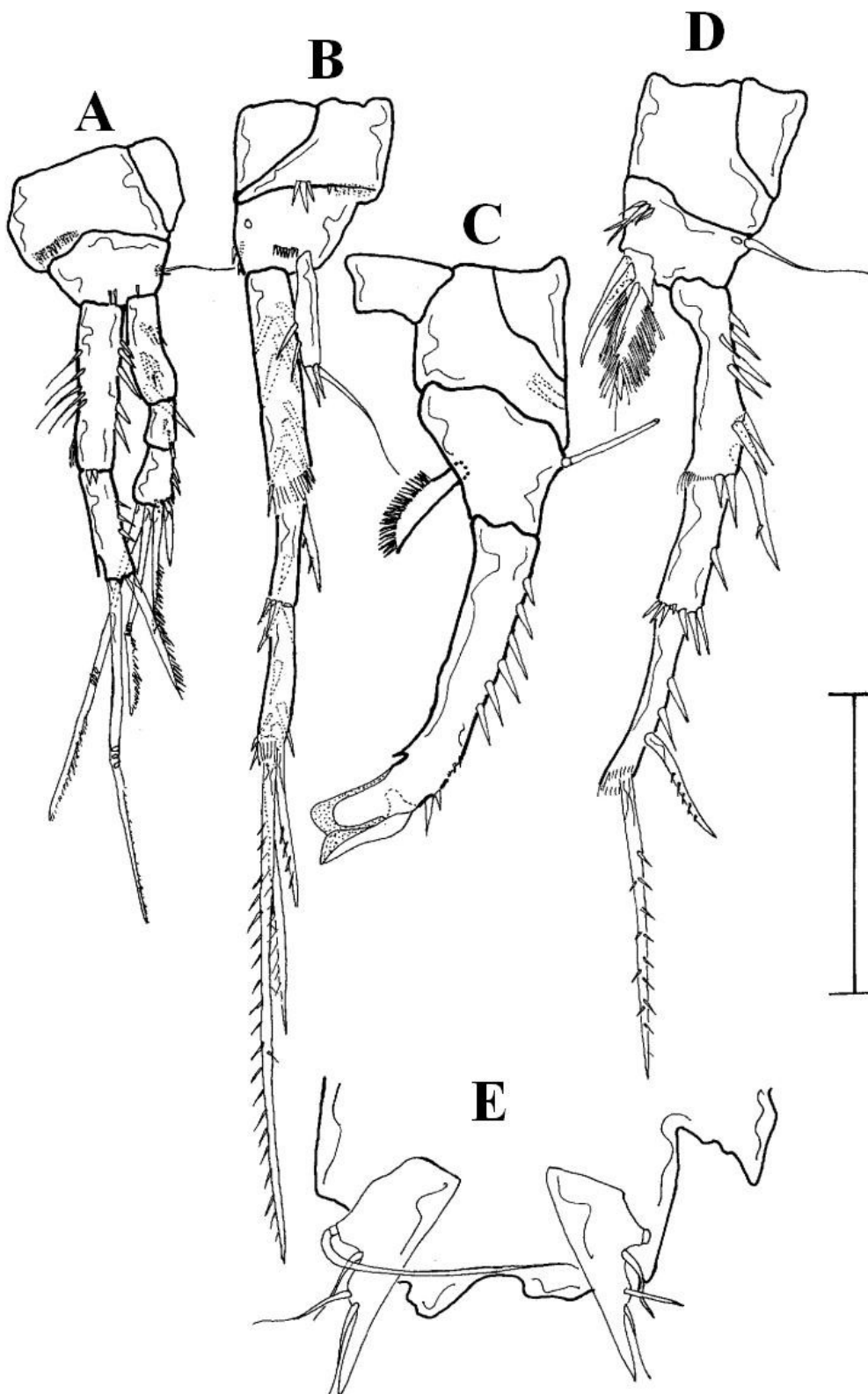


Figure 21- *Remaneicaris paraguayensis* (Noodt, 1963), male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar= 50 μ m.

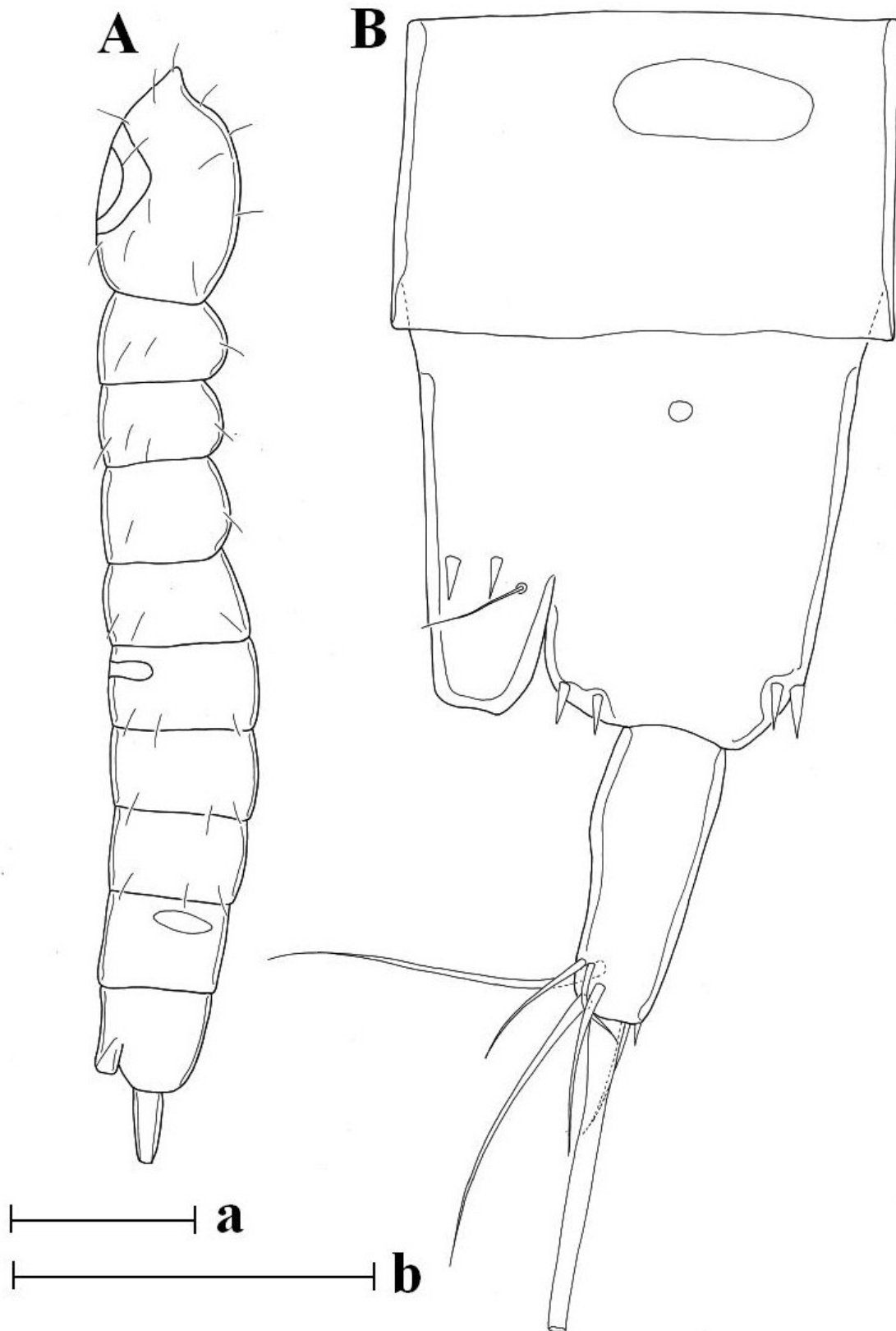


Figure 22- *Remaneicaris paraensis* (Noodt, 1963), male. A, habitus lateral; Scale bar a = 100 μ m . B, telson in a lateral view; Scale bar b= 50 μ m



Figure 23-*Remaneicaris paraensis* (Noodt, 1963), male. A, antennule; B, leg 1. Scale bar= 50 μ m.

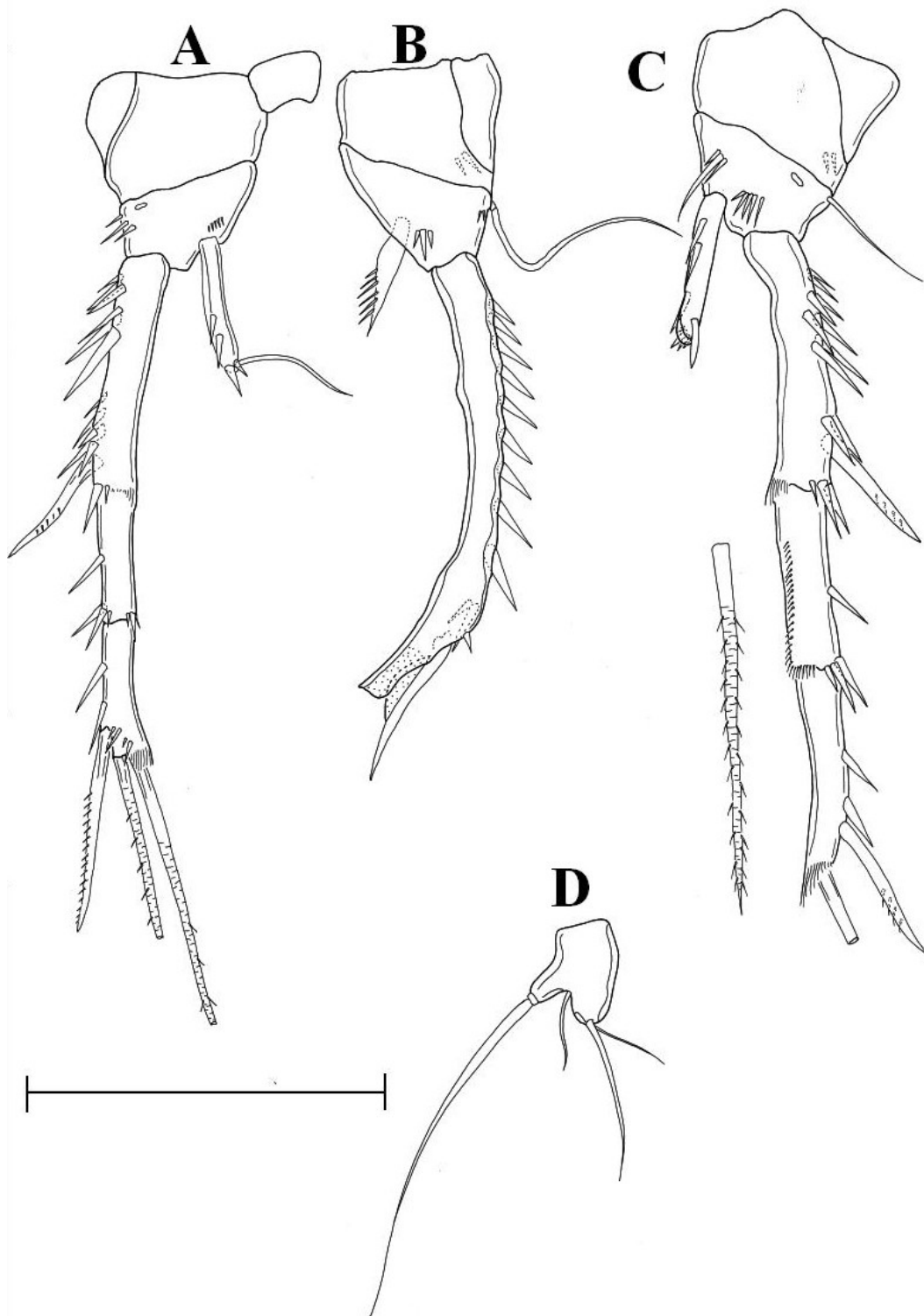


Figure 24- *Remaneicaris paraensis* (Noodt, 1963), male. A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bar= 50 μ m.

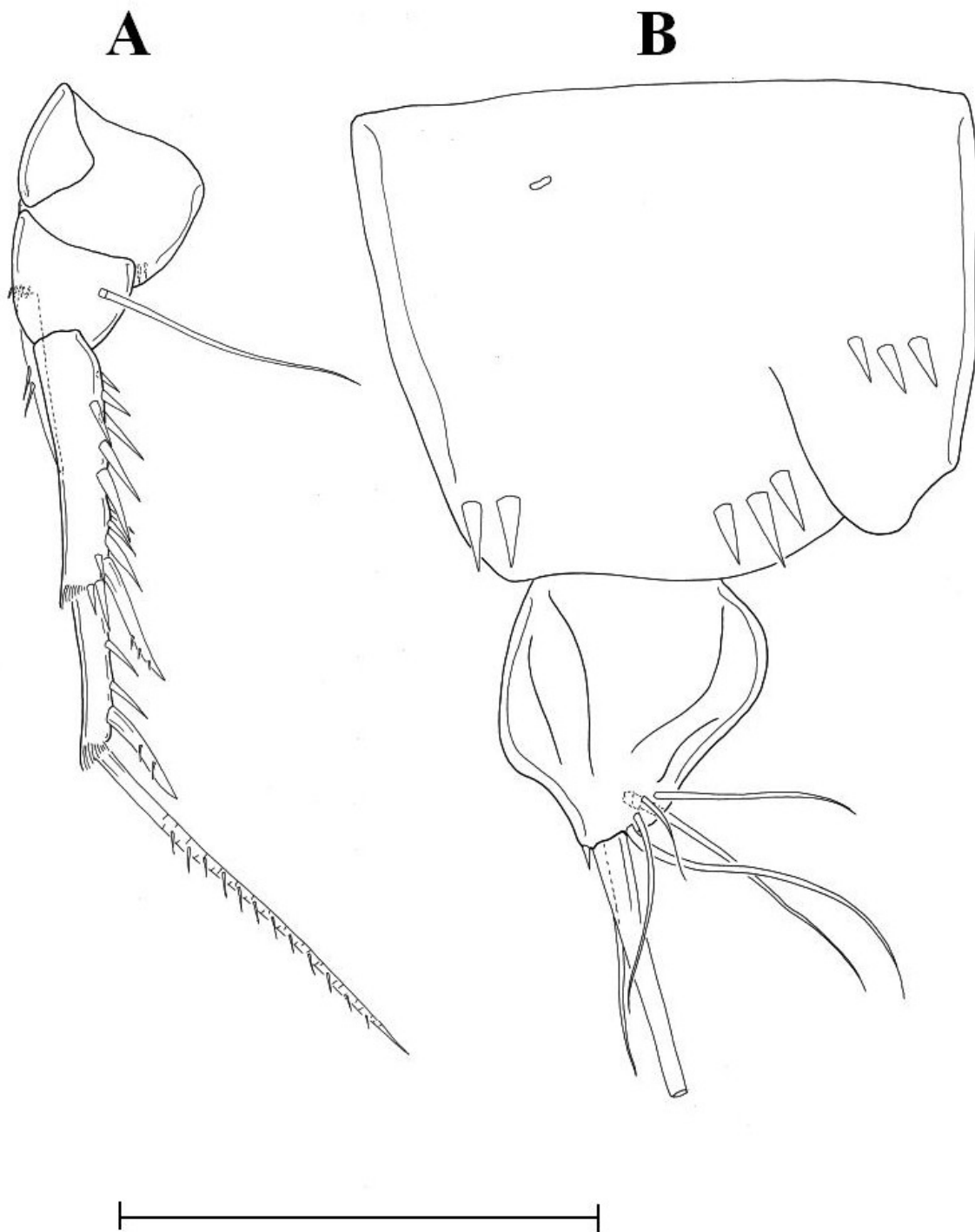


Figure 25- *Remaneicaris paraensis* f. *bulbifera* (Noodt, 1963). A, leg 3; B, telson in a lateral view. Scale bar= 50 μ m.

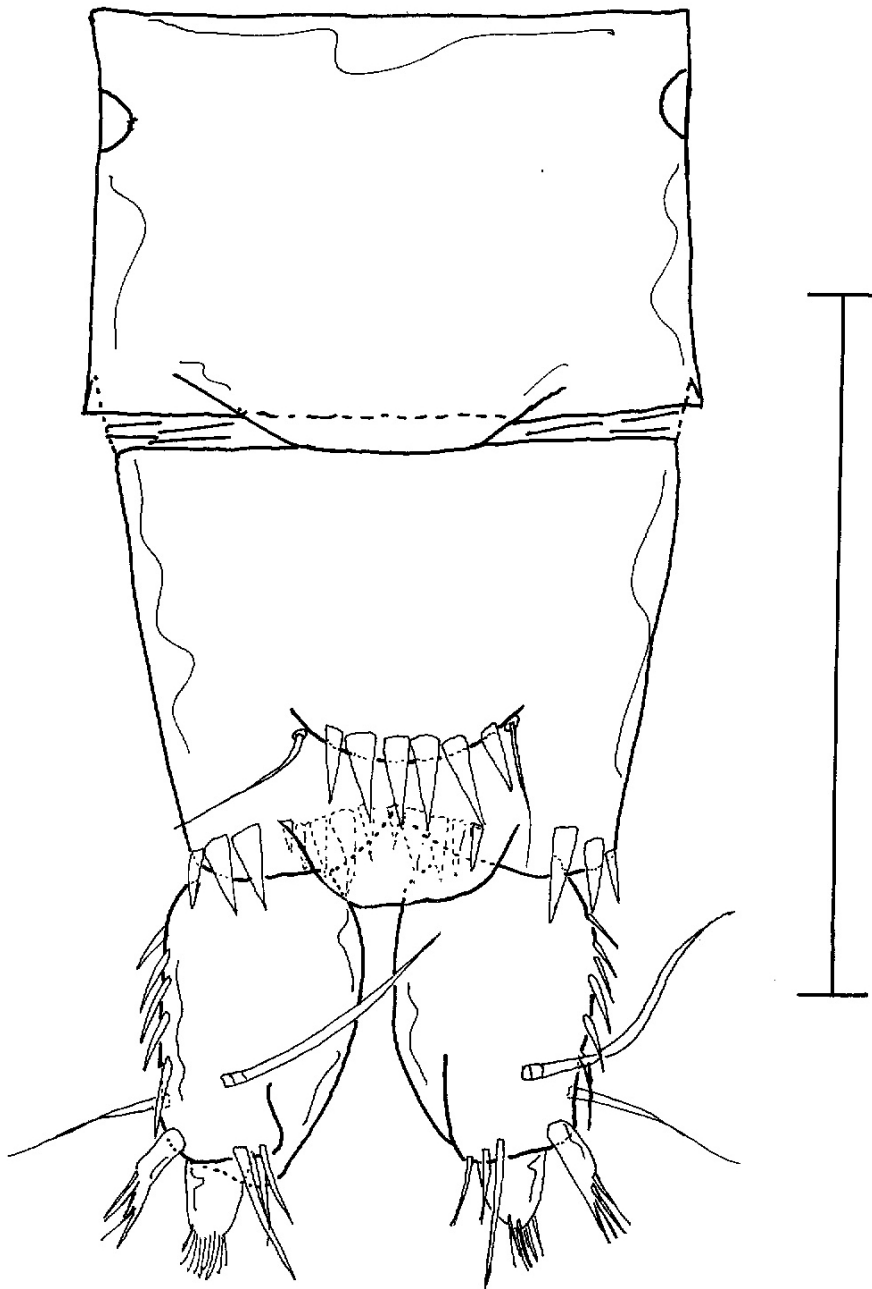


Figure 26- *Remaneicaris hexacantha* (Kiefer, 1936). telson and last urosomite in a dorsal view. Scale bar= 50 μ m.

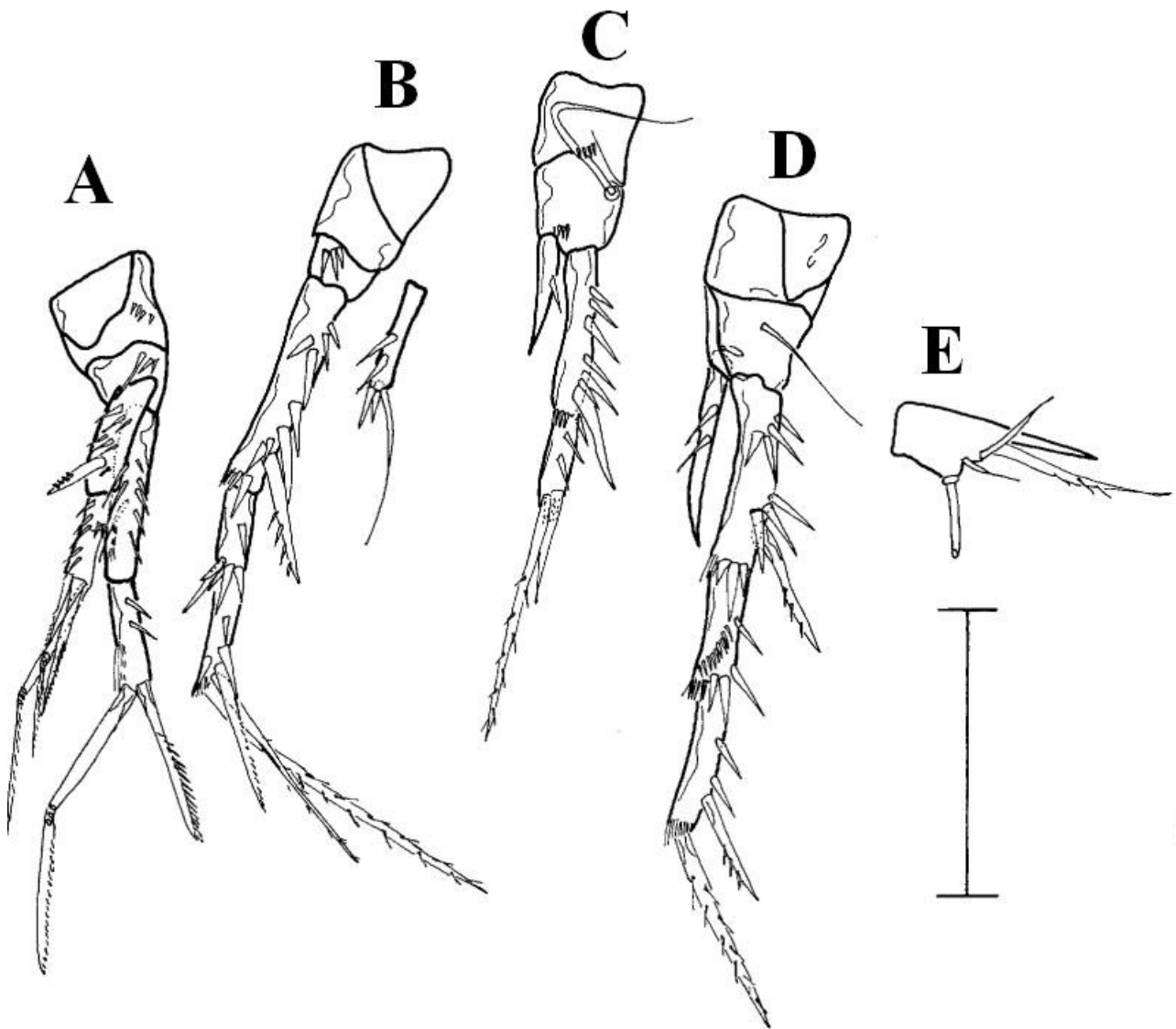


Figure 27- *Remaneicaris hexacantha* (Kiefer, 1936). A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar= 50 μ m.

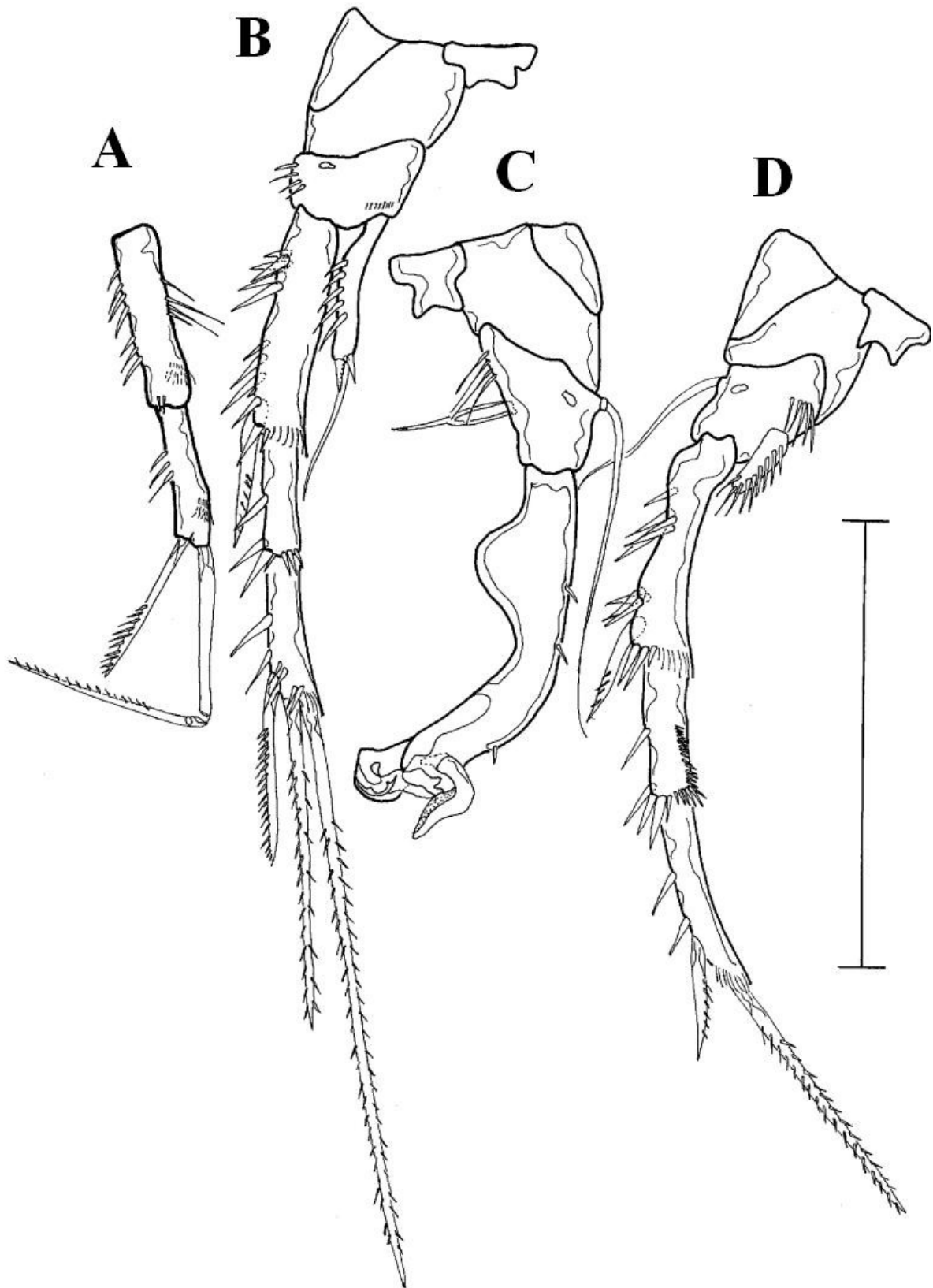


Figure 28- *Remaneicaris cordobaensis* (Noodt, 1965), male. A, end of leg 1; B, leg 2; C, leg 3; D, leg 4. Scale bar= 50 μ m.

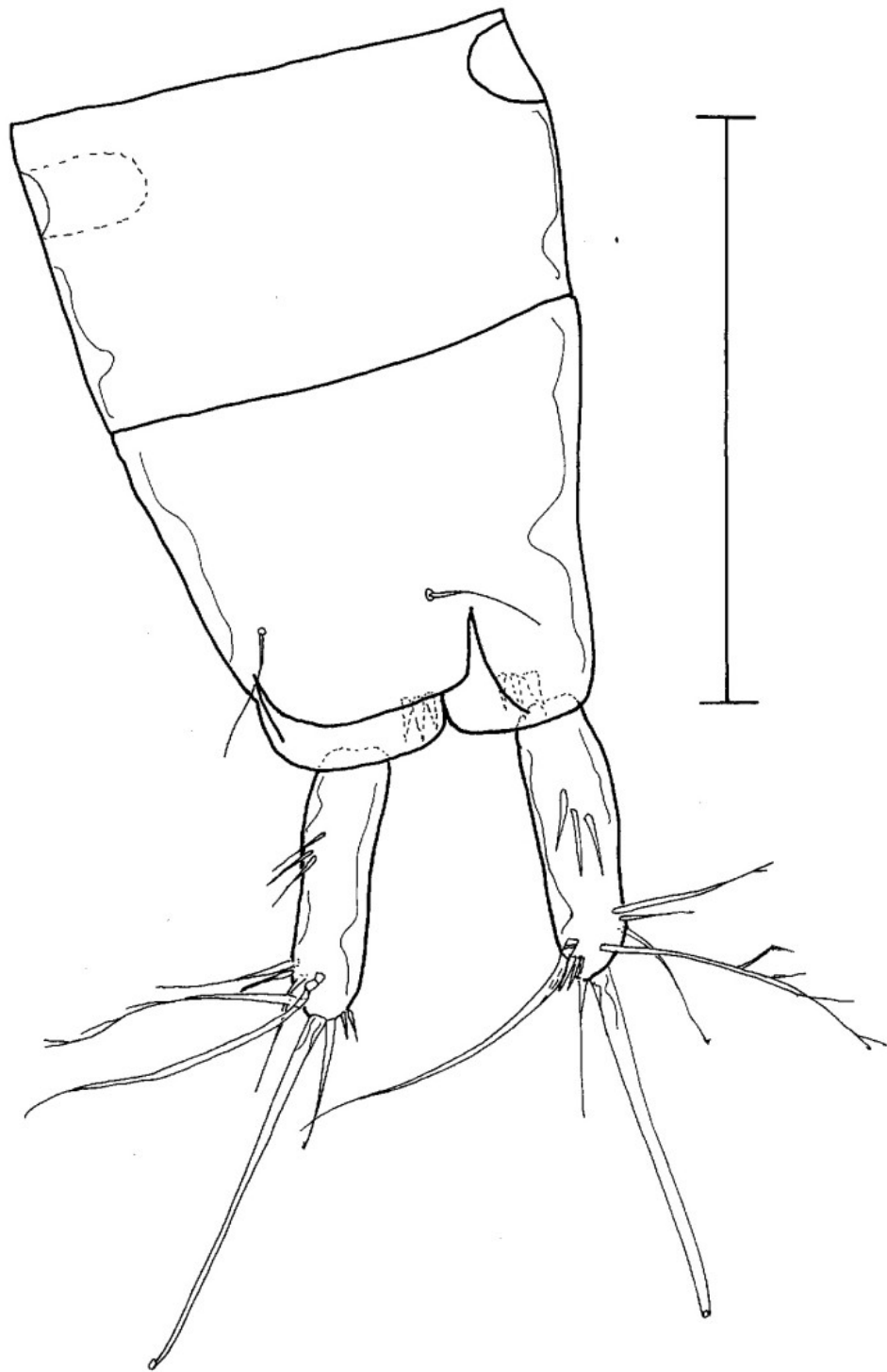


Figure 29- *Remaneicaris ciliata* (Noodt, 1965), male. telson in a dorsal view. Scale bar= 50 μ m.

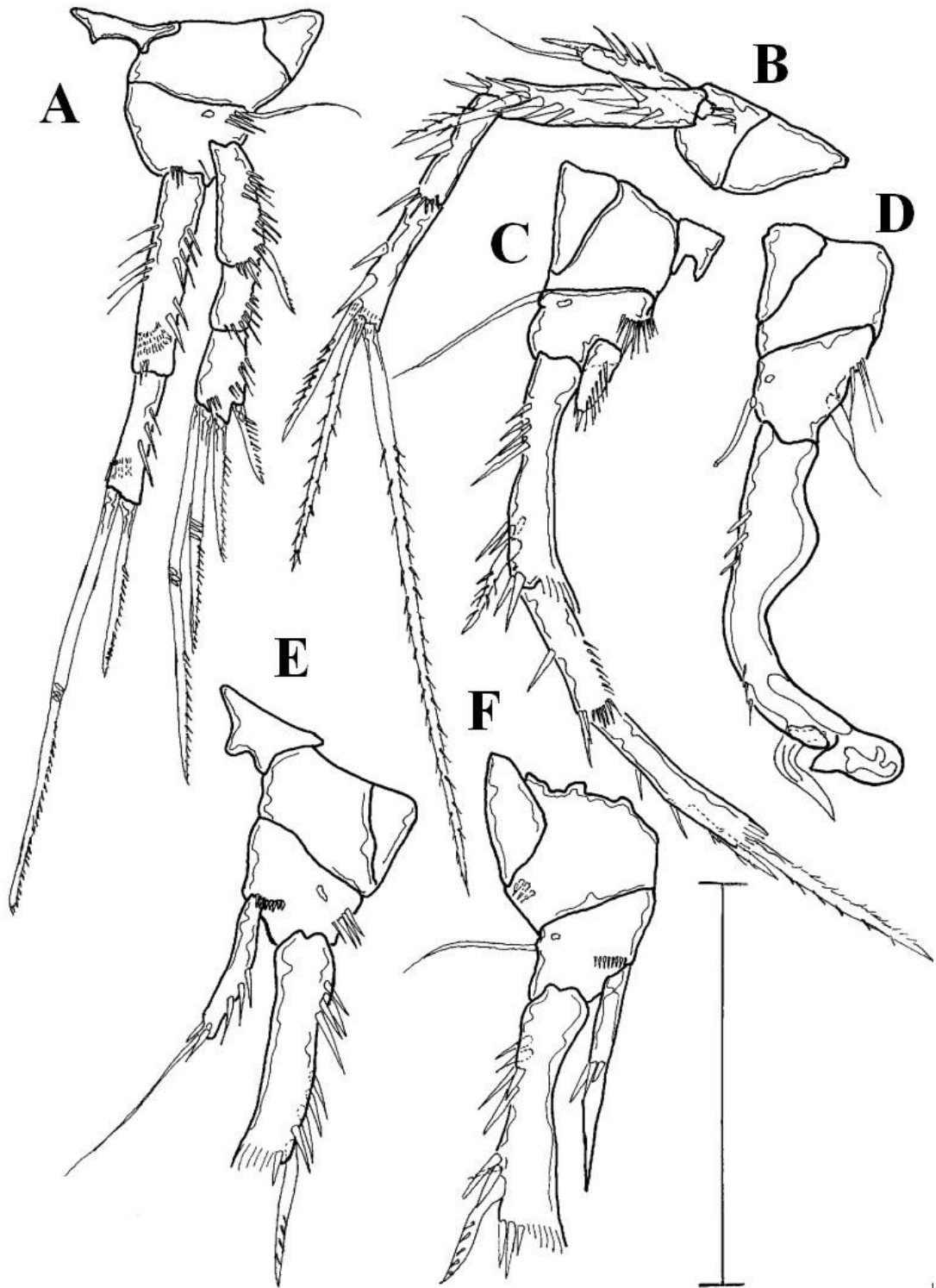


Figure 30- *Remaneicaris ciliata* (Noodt, 1965). Male; A, leg 1; B, leg 2; C, leg 3; D, leg 4. Female; E, leg 3; F, leg 4. Scale bar= 50 μ m.

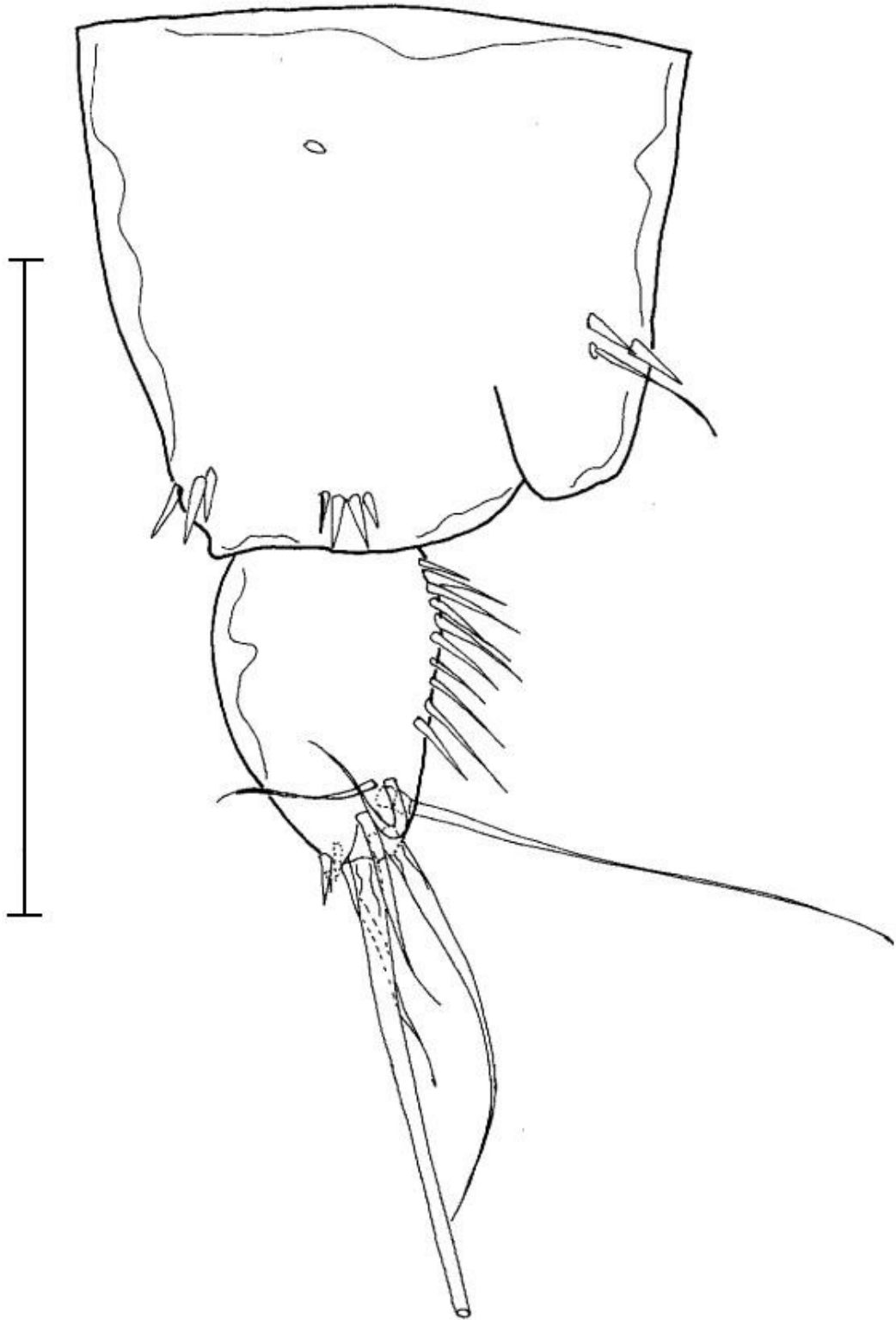


Figure 31- *Remaneicaris ciliata* (Noodt, 1965). telson and furca of female in a lateral view. Scale bar= 50 μ m.

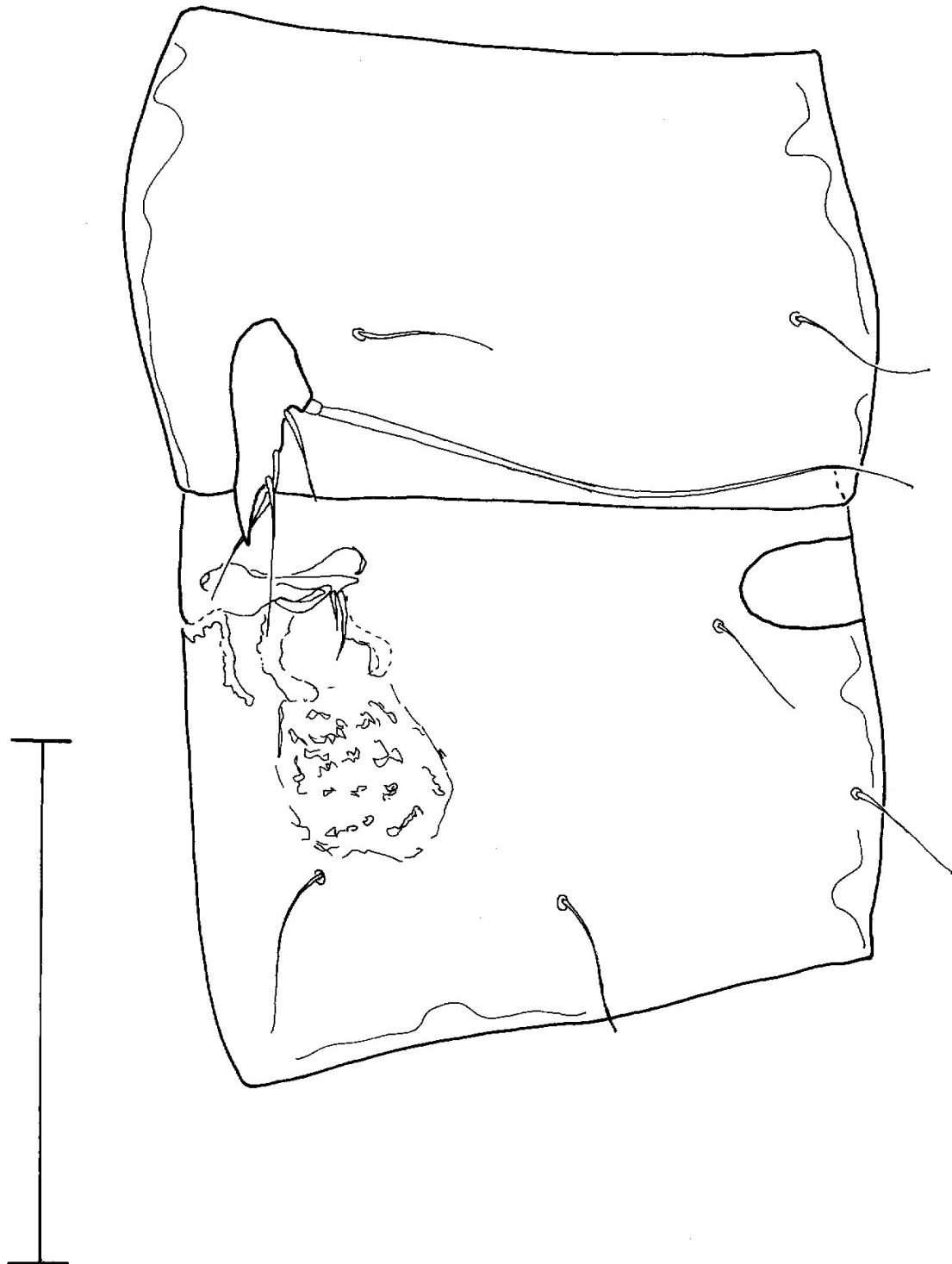


Figure 32- *Remaneicaris ciliata* (Noodt, 1965). First and second urosomites of female, with legs 5, 6 and genital structure. Scale bar= 50 μ m.

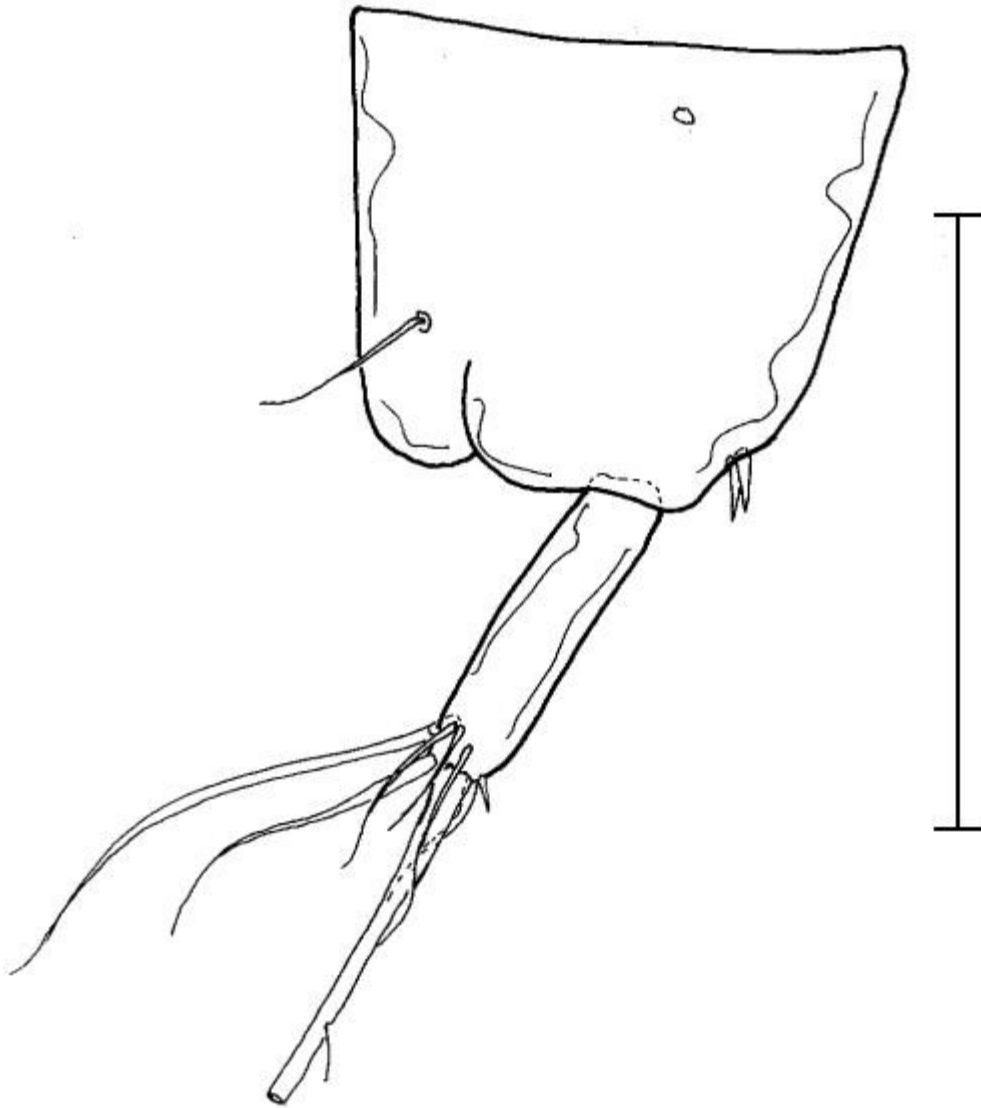


Figure 33- *Remaneicaris sierrae* (Noodt, 1965). telson of male in a lateral view. Scale bar= 50 μ m.

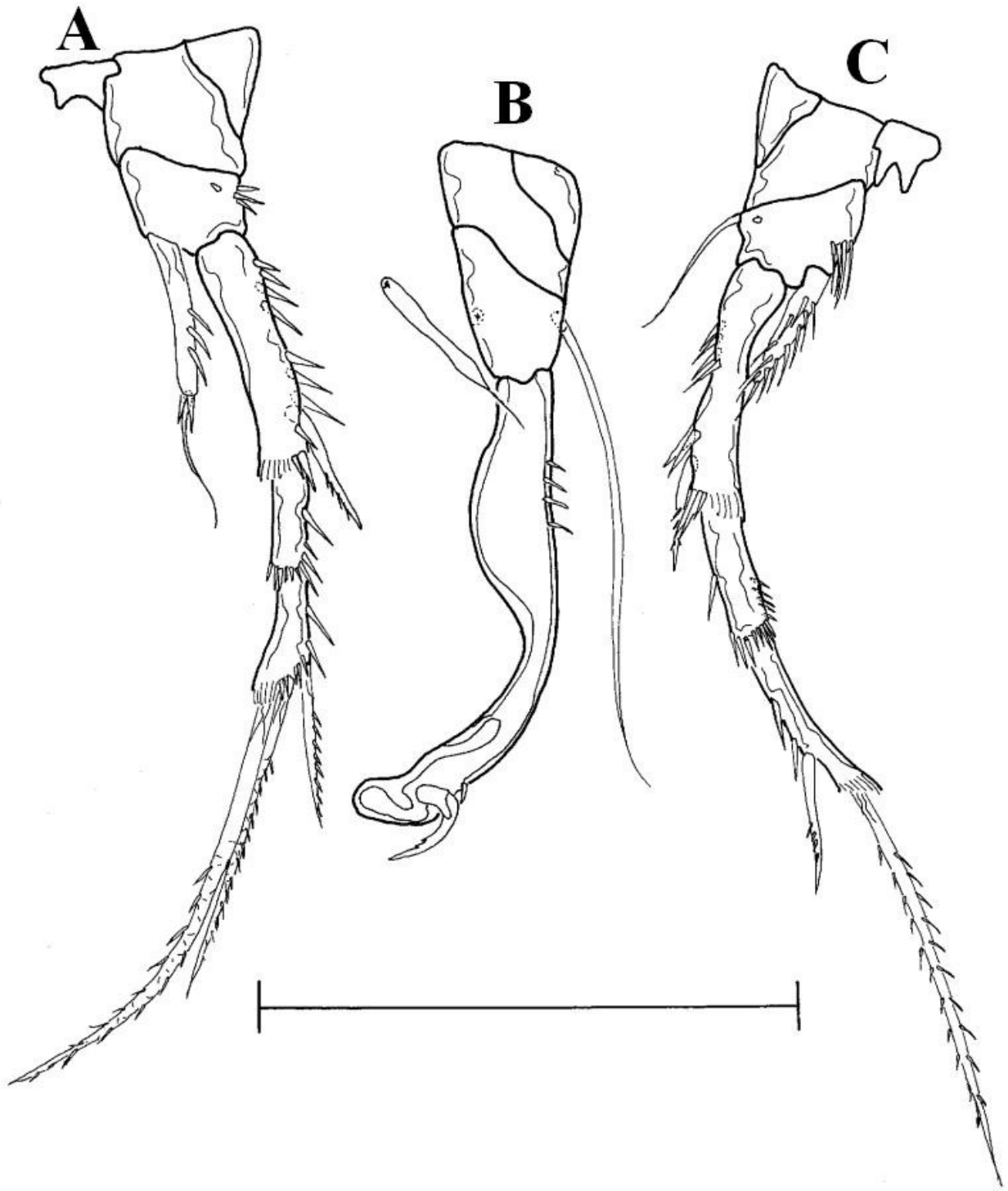


Figure 34- *Remaneicaris sierrae* (Noodt, 1965). Male; A, leg 2; B, leg 3; C, leg 4. Scale bar= 50 μ m.

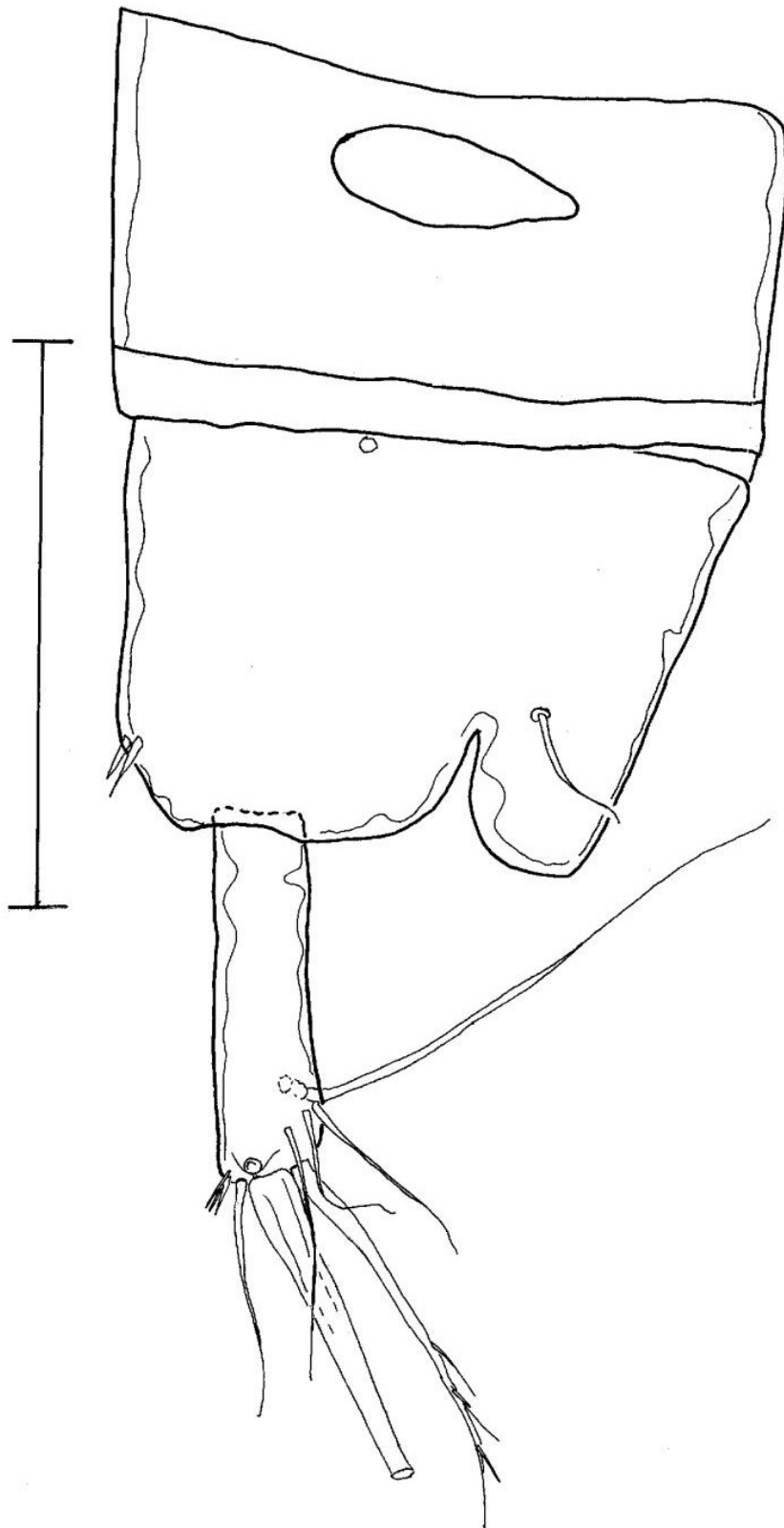


Figure 35- *Remaneicaris sanctiludovici* (Noodt, 1965). Male; telson in lateral view. Scale bar= 50 μ m.

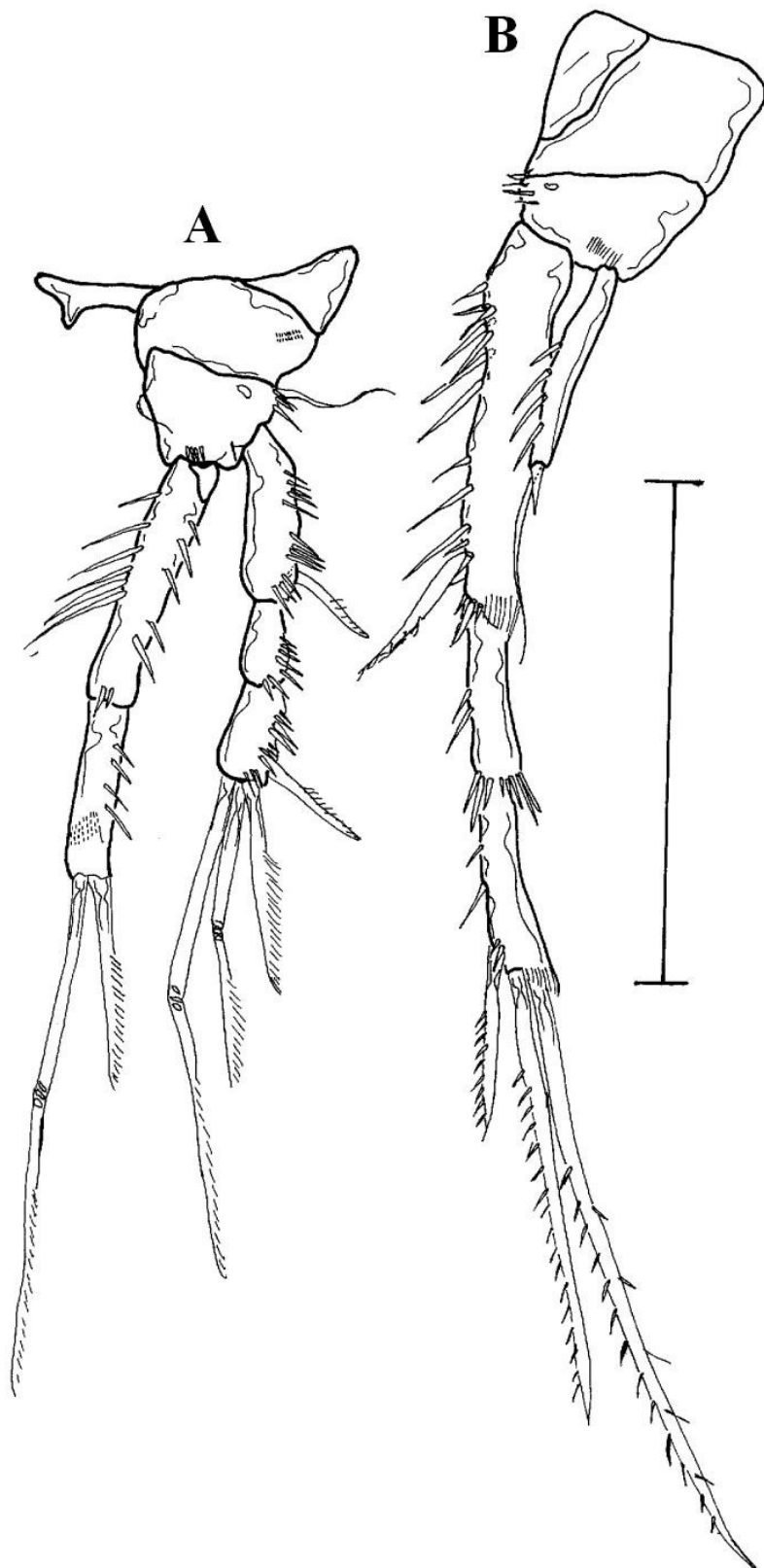


Figure 36- *Remaneicaris sanctiludovici* (Noodt, 1965). Male; A, leg 1; B, leg 2. Scale bar= 50 μ m.

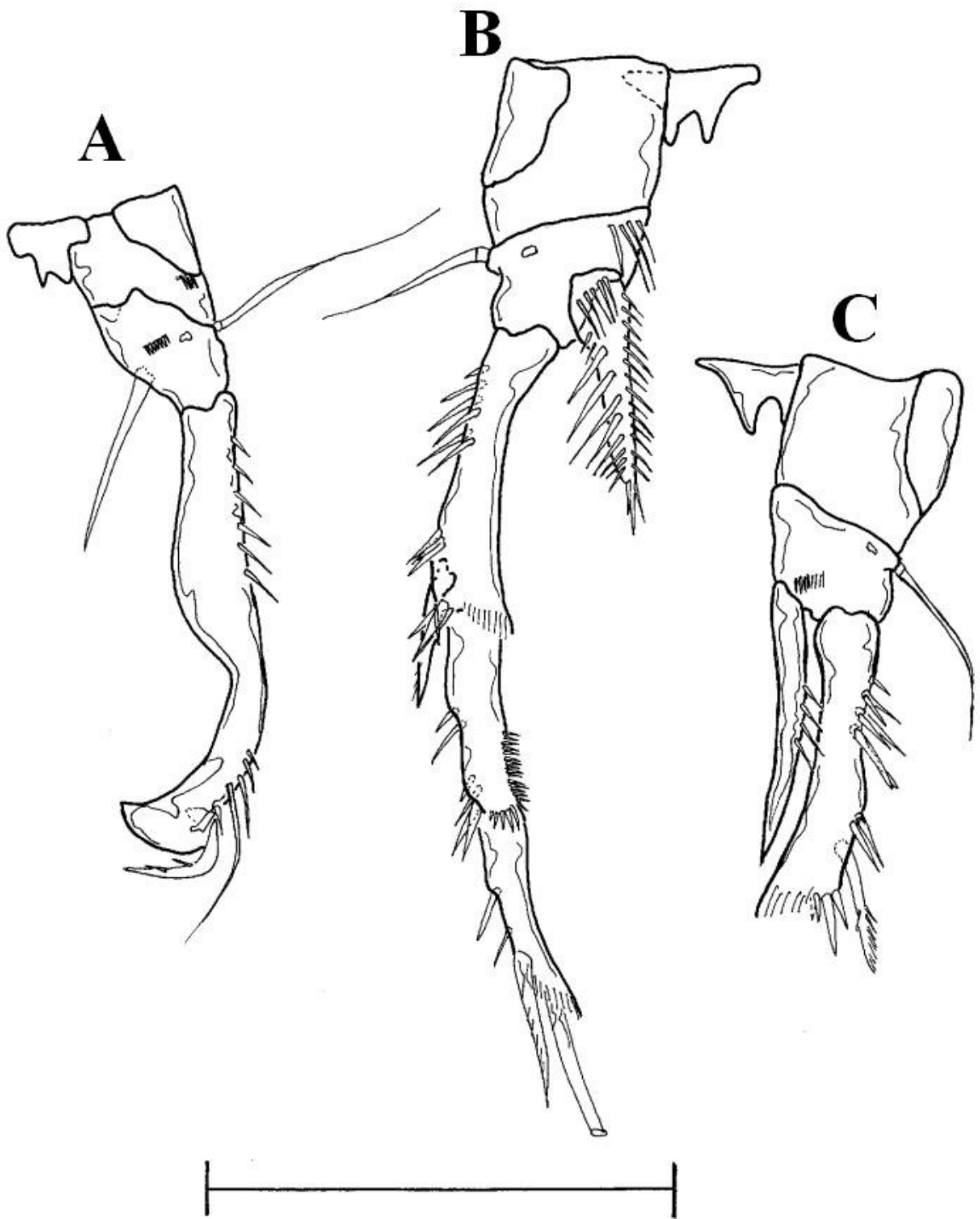


Figure 37- *Remaneicaris sanctiludovici* (Noodt, 1965). Male; A, leg 3; B, leg 4. Female; C, leg 4 of female. Scale bar= 50 μ m.

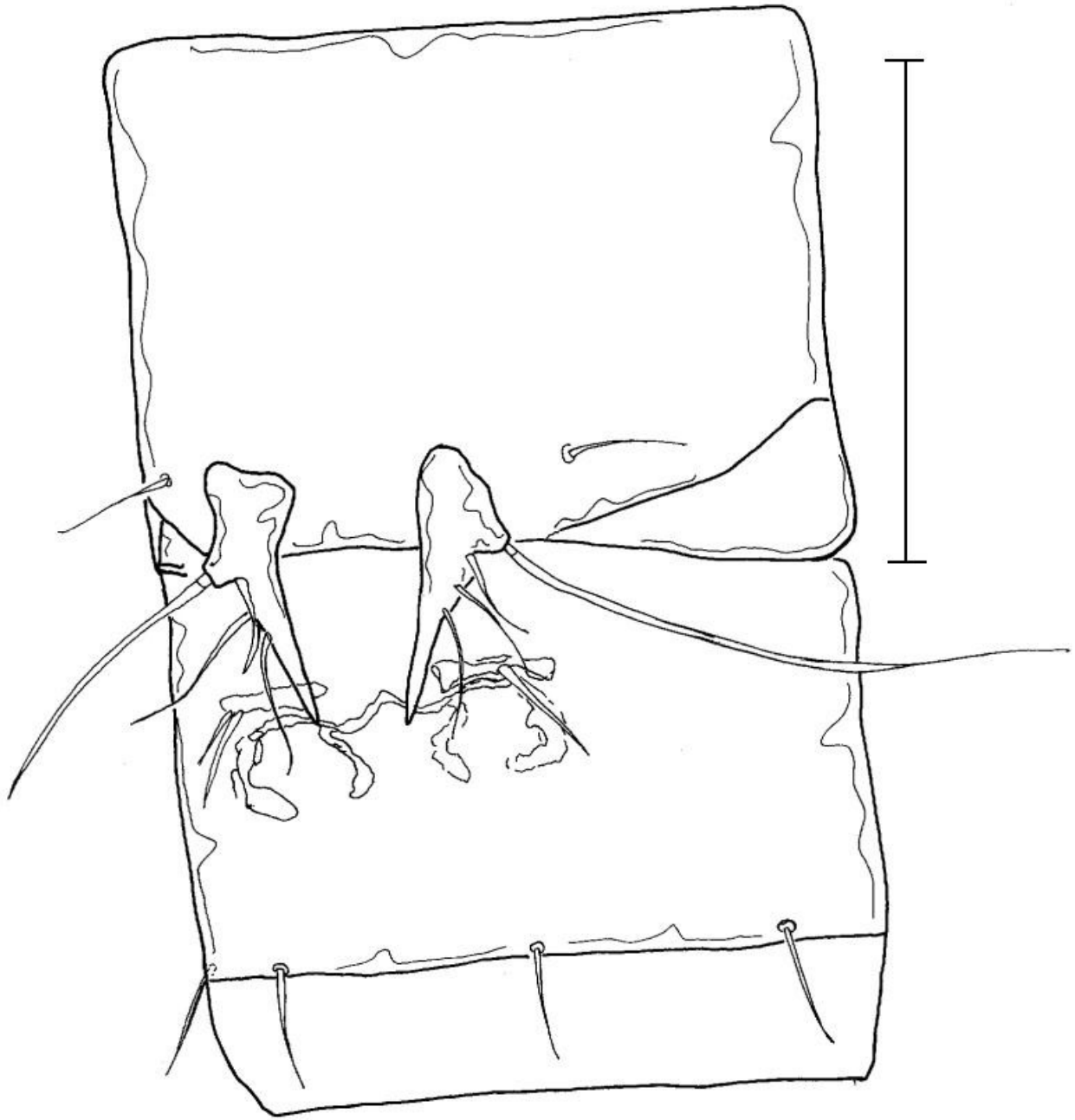


Figure 38- *Remaneicaris sanctiludovici* (Noodt, 1965). First and second urosomite of female with legs 5, 6 and genital structure. Scale bar= 50 μ m.

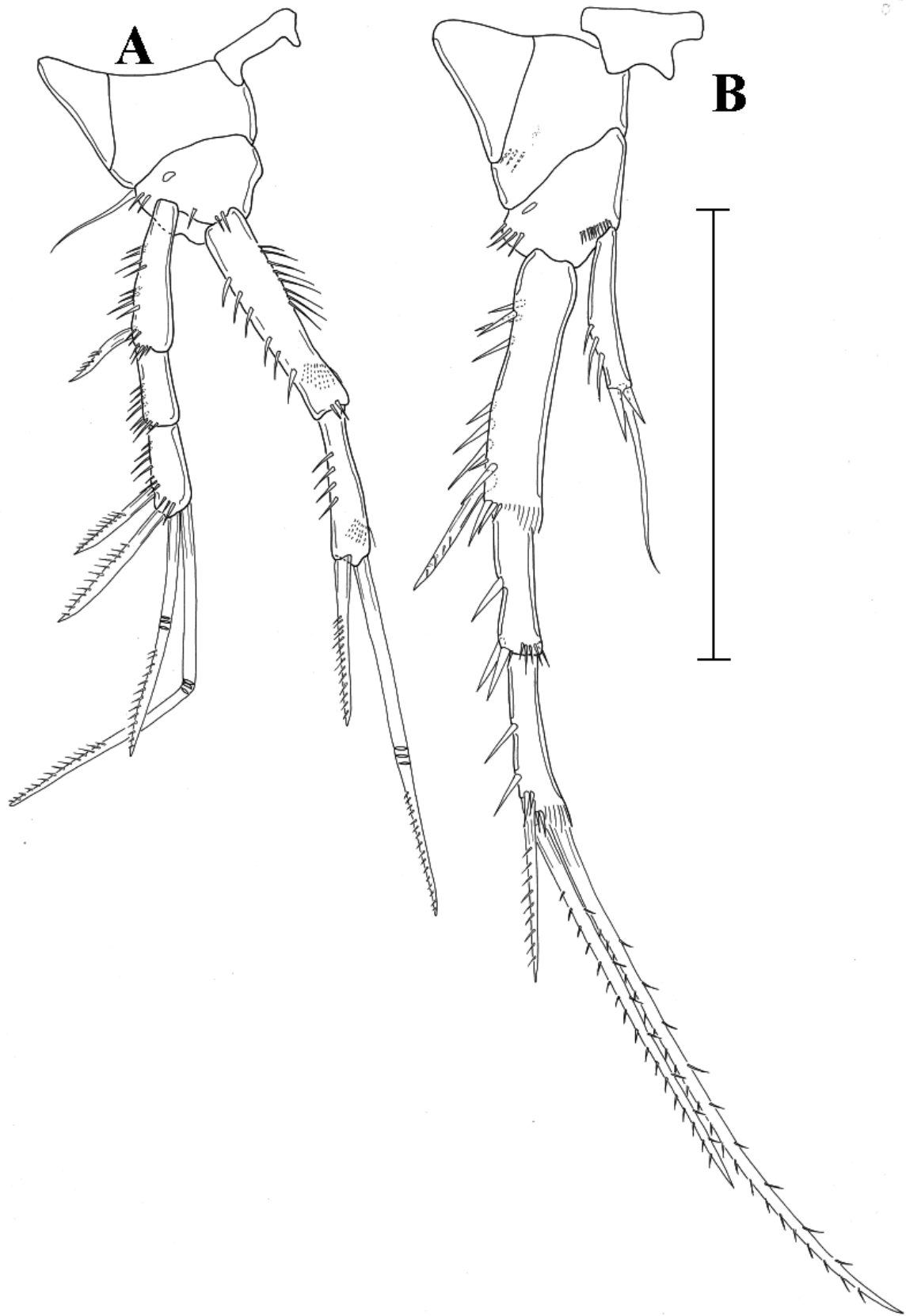


Figure 39- *Remaneicaris persephone* (Noodt, 1965). Male; A, leg 1; B, leg 2. Scale bar= 50 μ m.

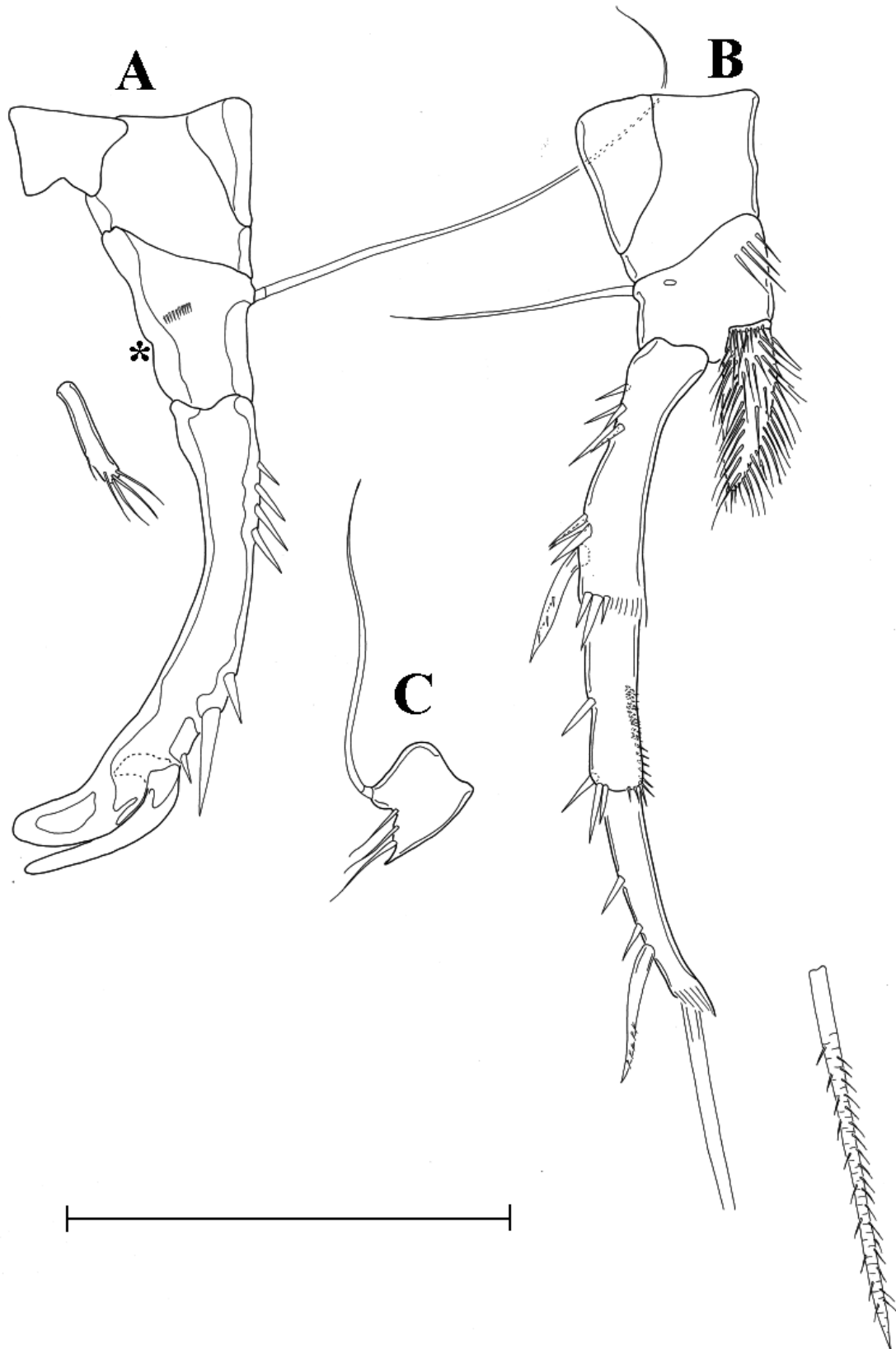


Figure 40- *Remaneicaris persephone* (Noodt, 1965). Male; A, leg 3; B, leg 4; C, leg 5. Symbol indicates the point of enp insertion. Scale bar= 50 μ m.

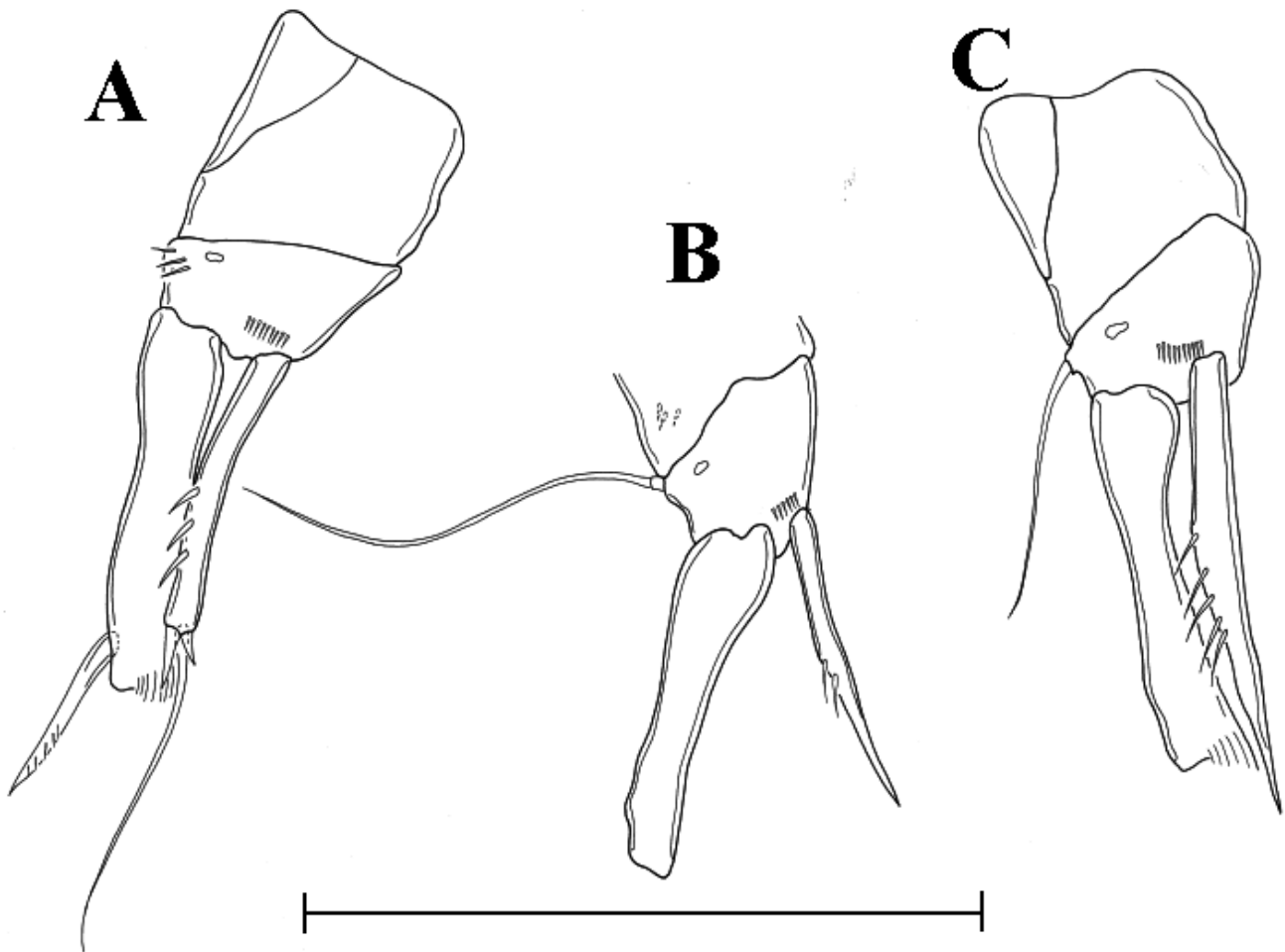


Figure 41- *Remaneicaris persephone* (Noodt, 1965). Female; A, leg 2; B, leg 3; C, leg 4. Scale bar= 50 μ m.

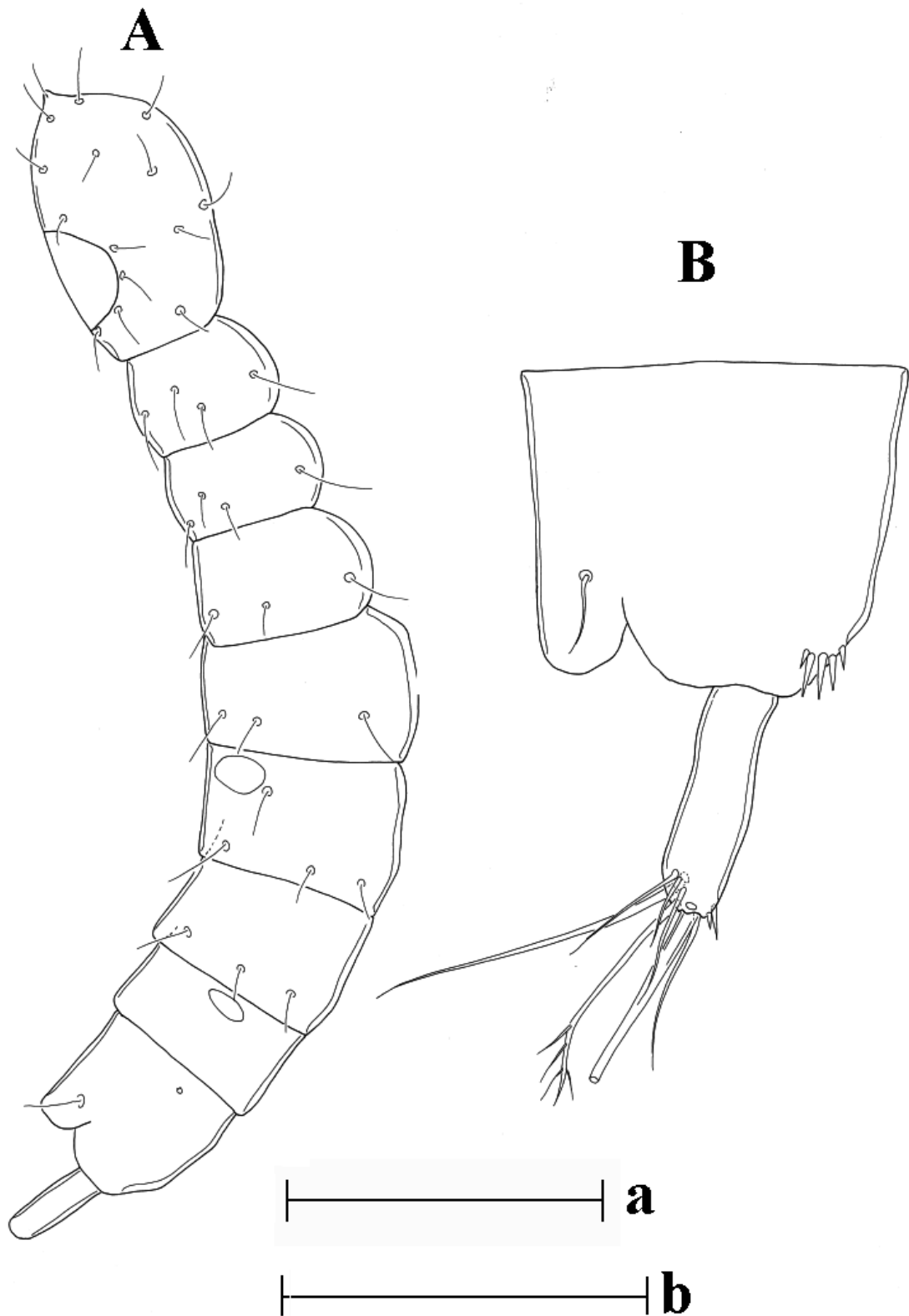


Figure 42- *Remaneicaris hecate* (Noodt, 1965). Male; A, habitus lateral, Scale bar b= 100 μ m. B, telson in a lateral view, Scale bar a= 50 μ m.

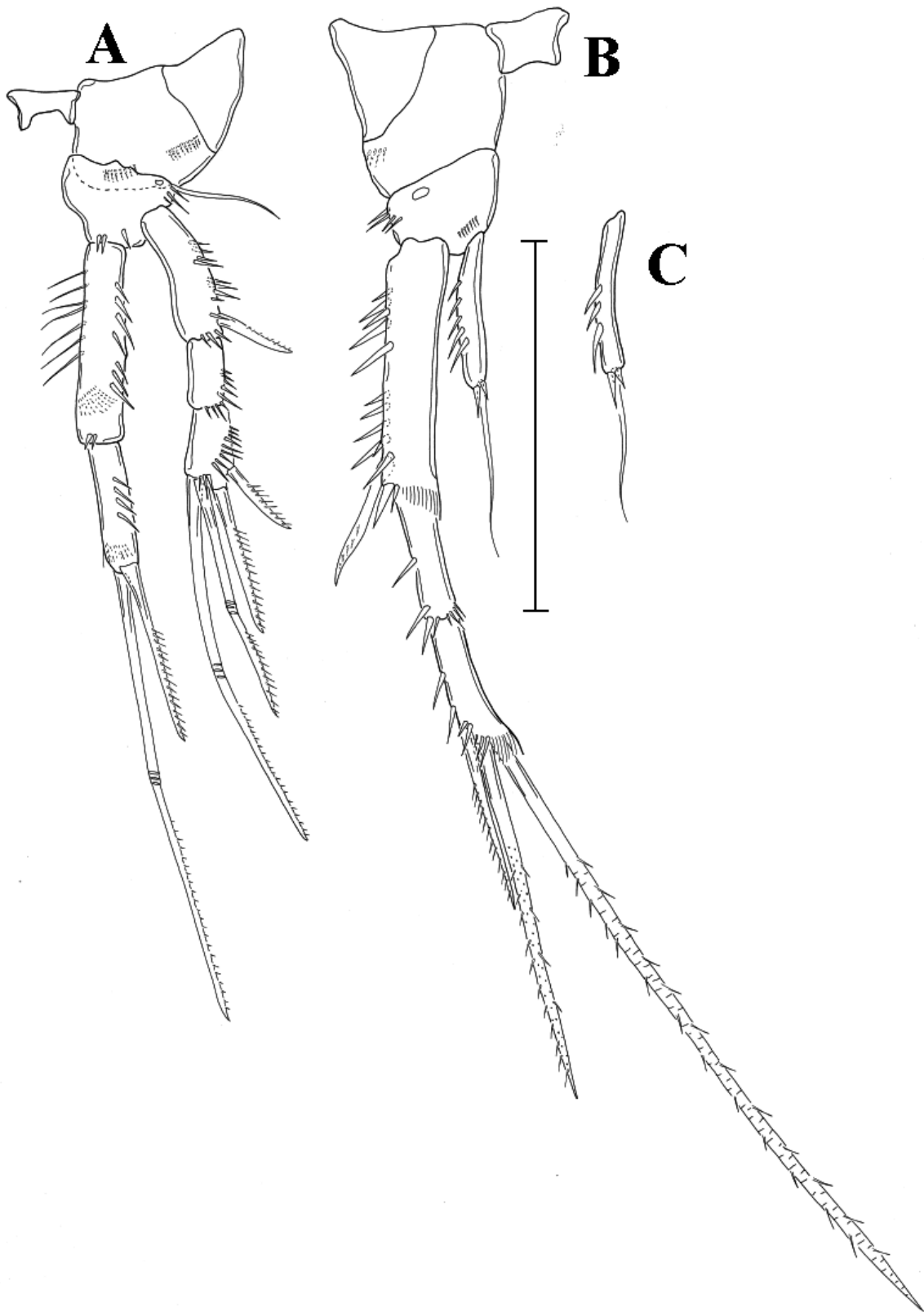


Figure 43- *Remaneicaris hecate* (Noodt, 1965). Male; A, leg 1; B, leg 2. Scale bar= 50 μ m.

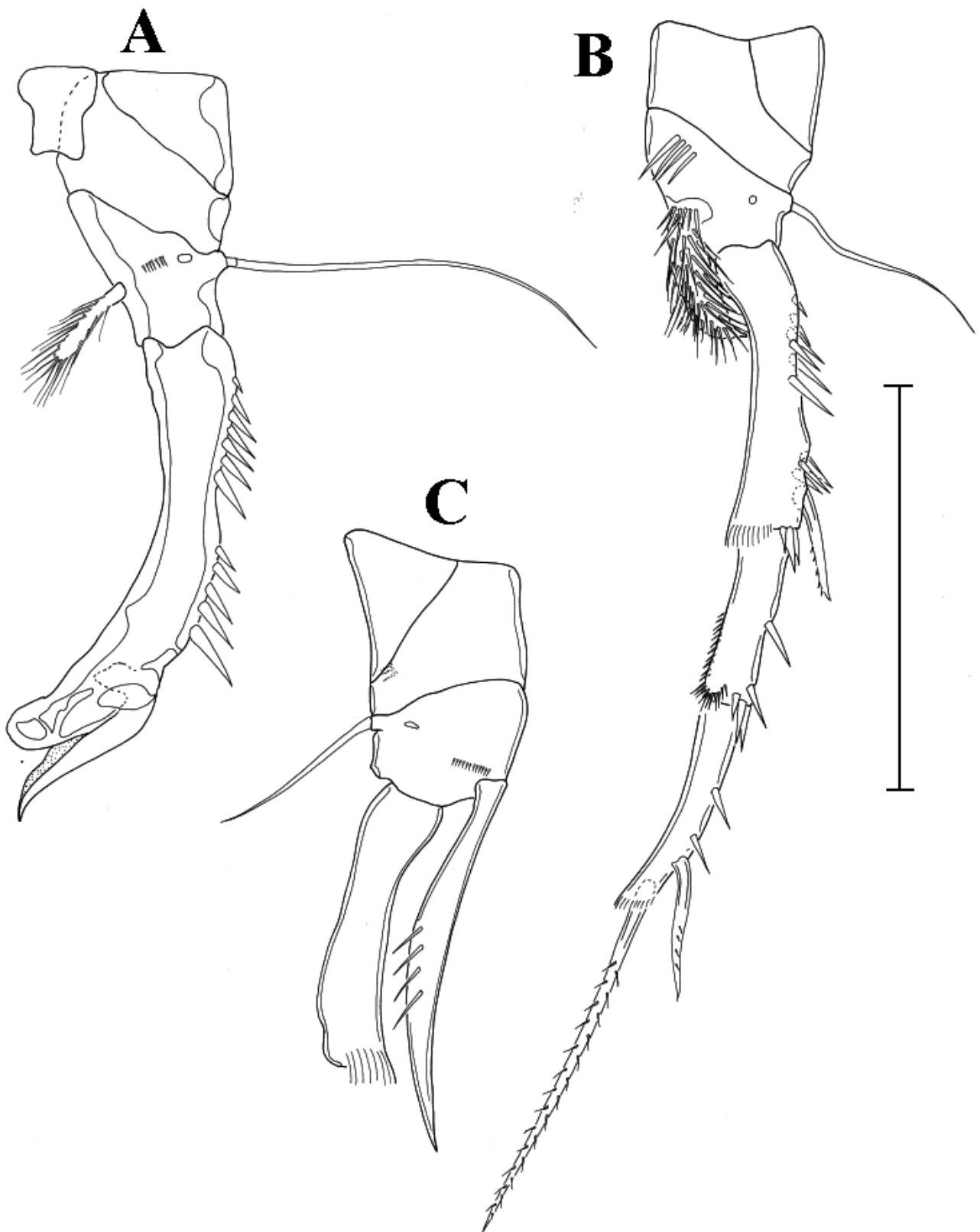


Figure 44- *Remaneicaris hecate* (Noodt, 1965). Male; A, leg 3; B, leg 4. Female, C; leg 4. Scale bar= 50 μ m.

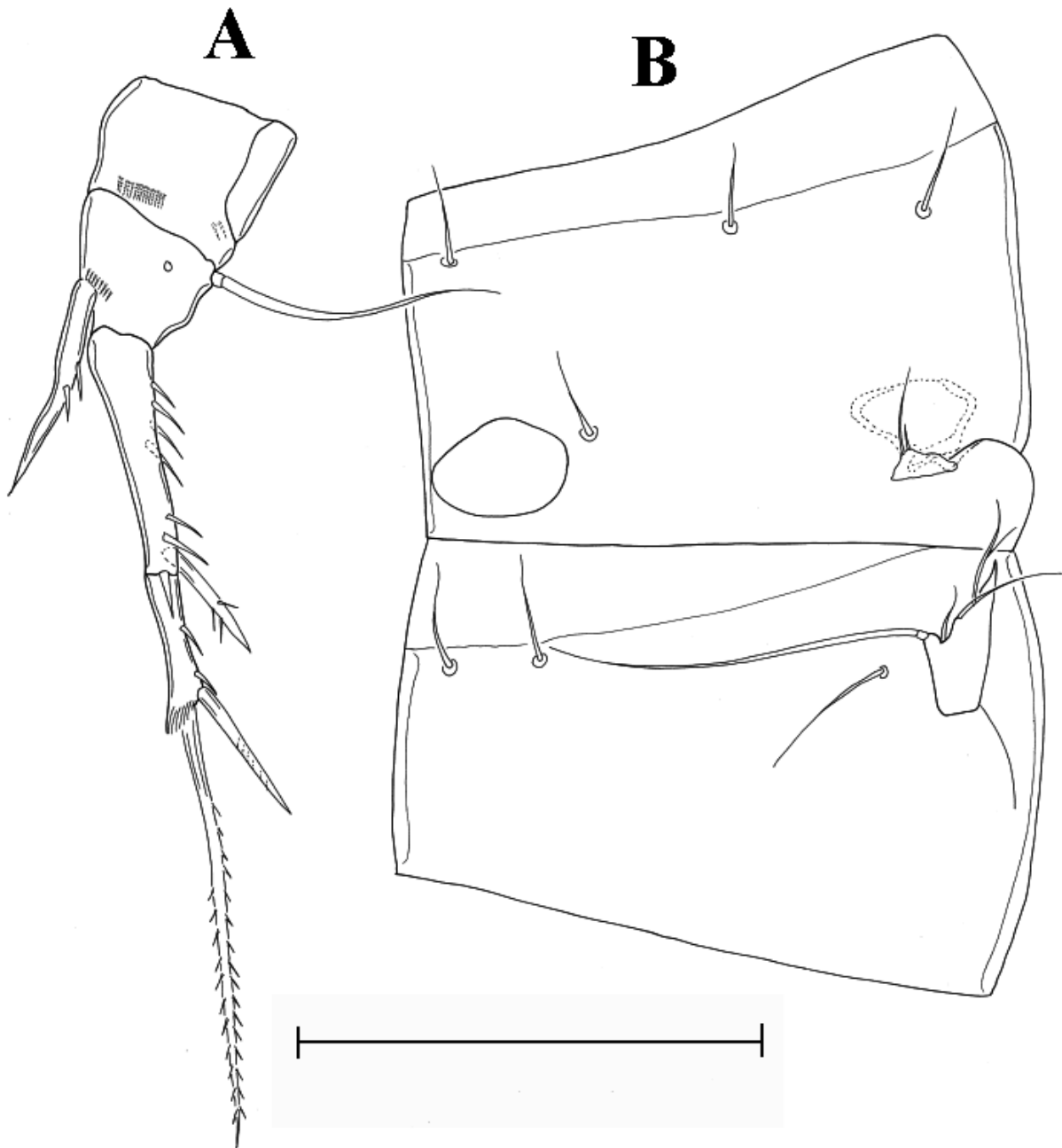


Figure 45- *Remaneicaris hecate* (Noodt, 1965). Female; A, leg 3; B, First and second urosomite with legs 5, 6 and genital structure. Scale bar= 50 μ m.

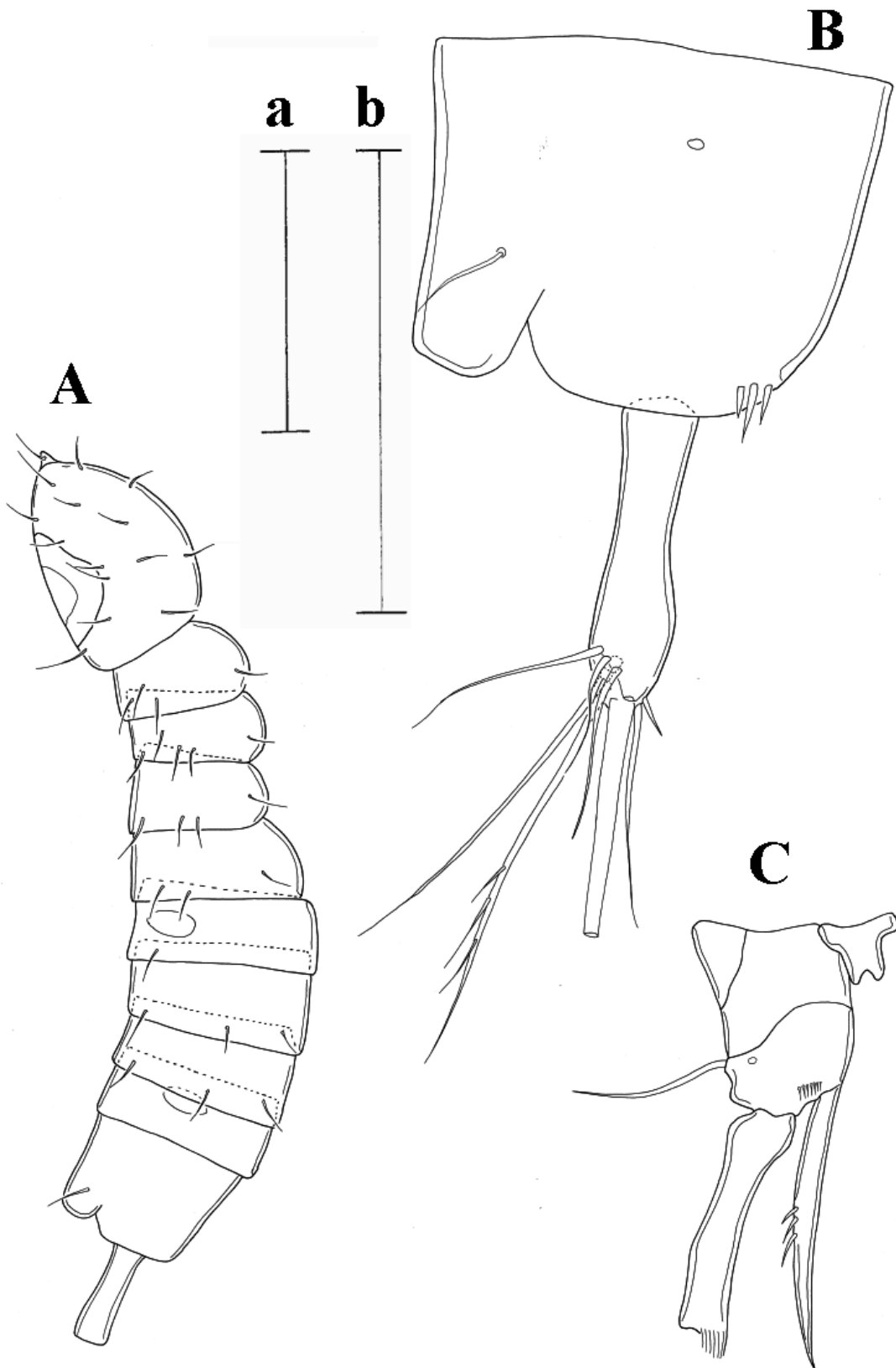


Figure 46- *Remaneicaris pluto* (Noodt, 1965). Male; A, habitus lateral; Scale bar a= 100 μ m.; B, telson in a dorsal view. Female; C, leg 4. Scale bar b= 50 μ m.

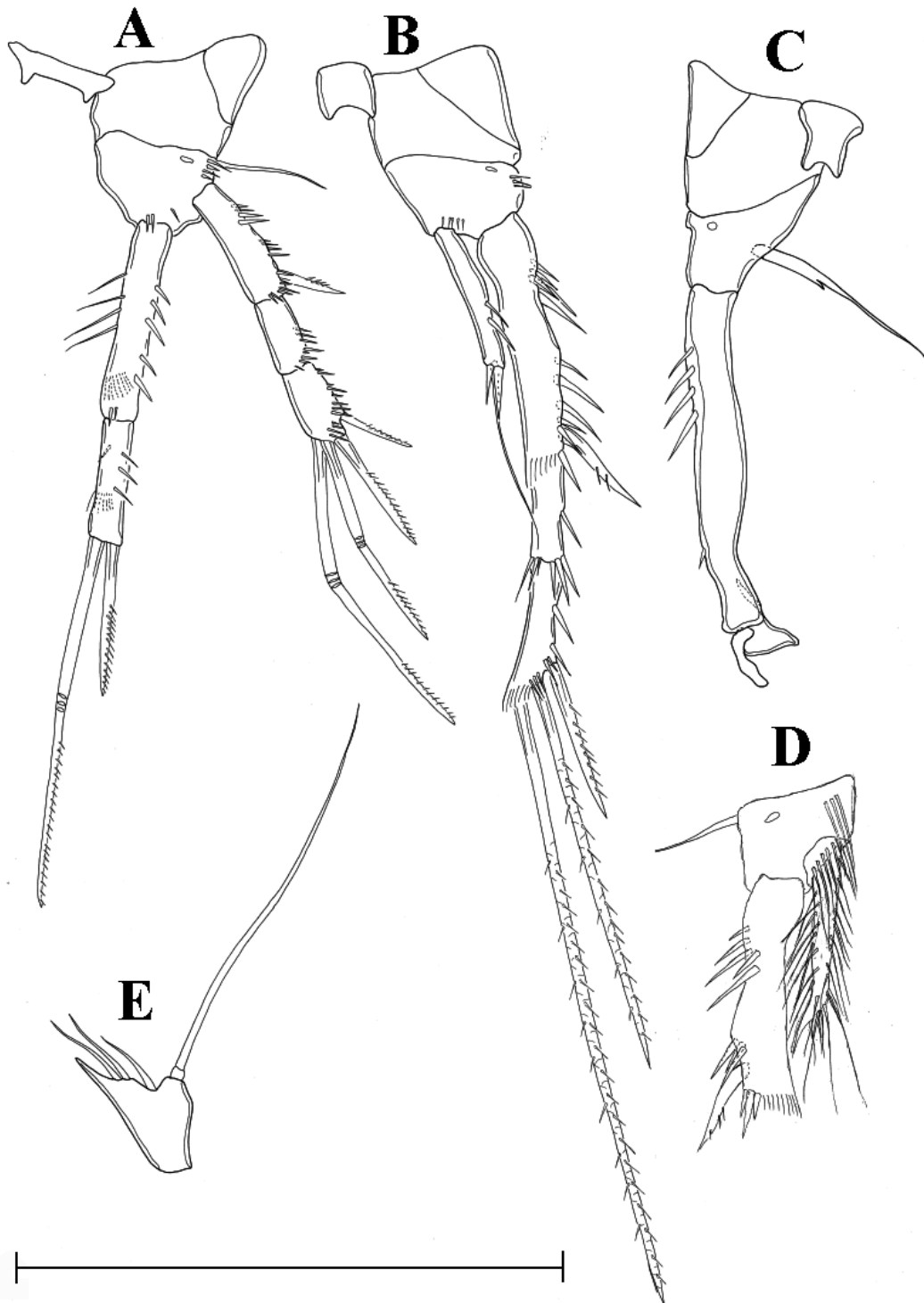


Figure 47- *Remaneicaris pluto* (Noodt, 1965). Male; A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bar= 50 μ m.

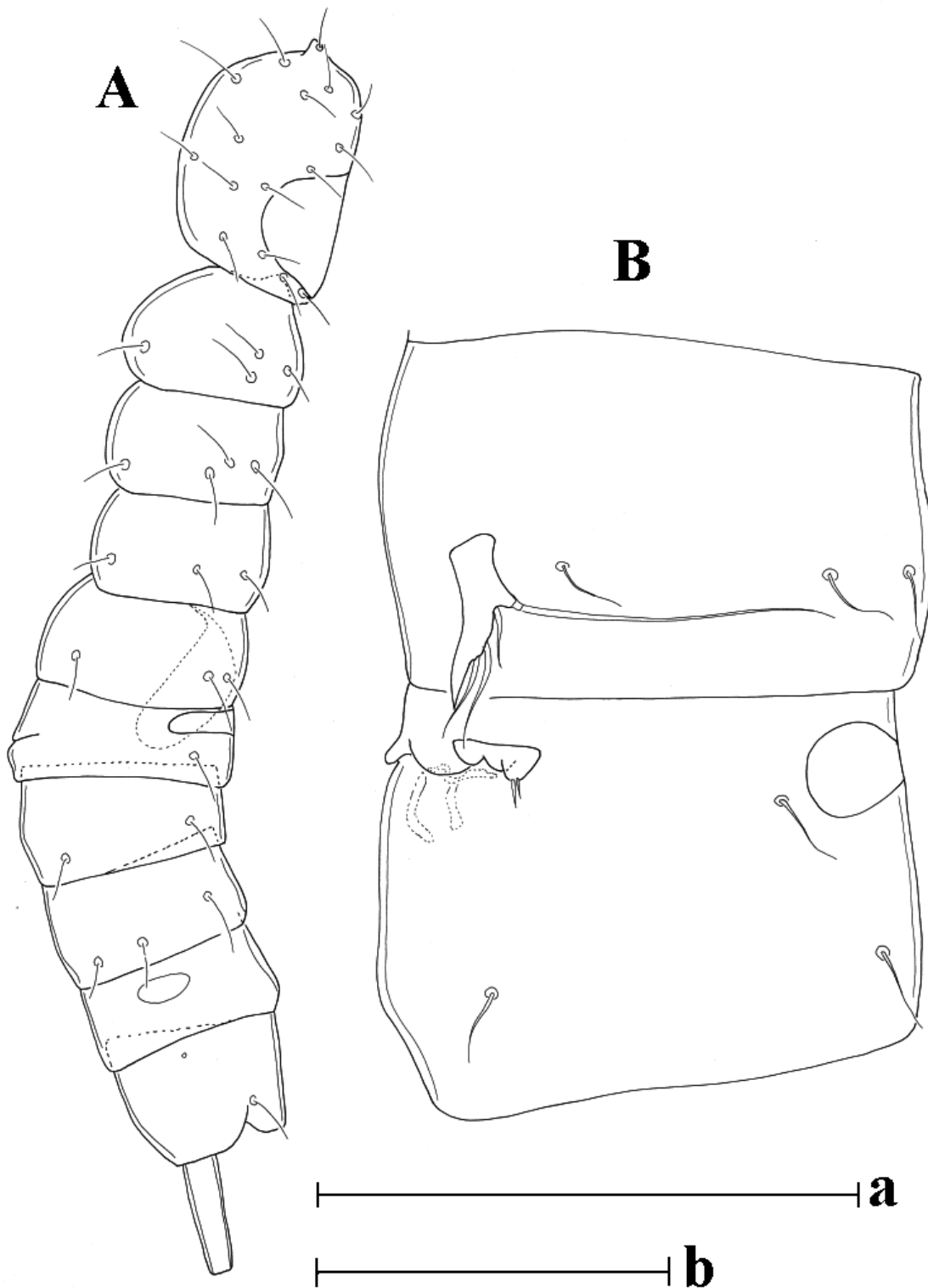


Figure 48- *Remaneicaris oncophora* (Noodt, 1965). A, lateral habitus of male; Scale bar b= 100 μ m. B, First and second urosomites of female with legs 5, 6 and genital structure. Scale bar a= 50 μ m.



Figure 49- *Remaneicaris oncophora* (Noodt, 1965). Antennule of male. Scale bar a= 25 μ m.

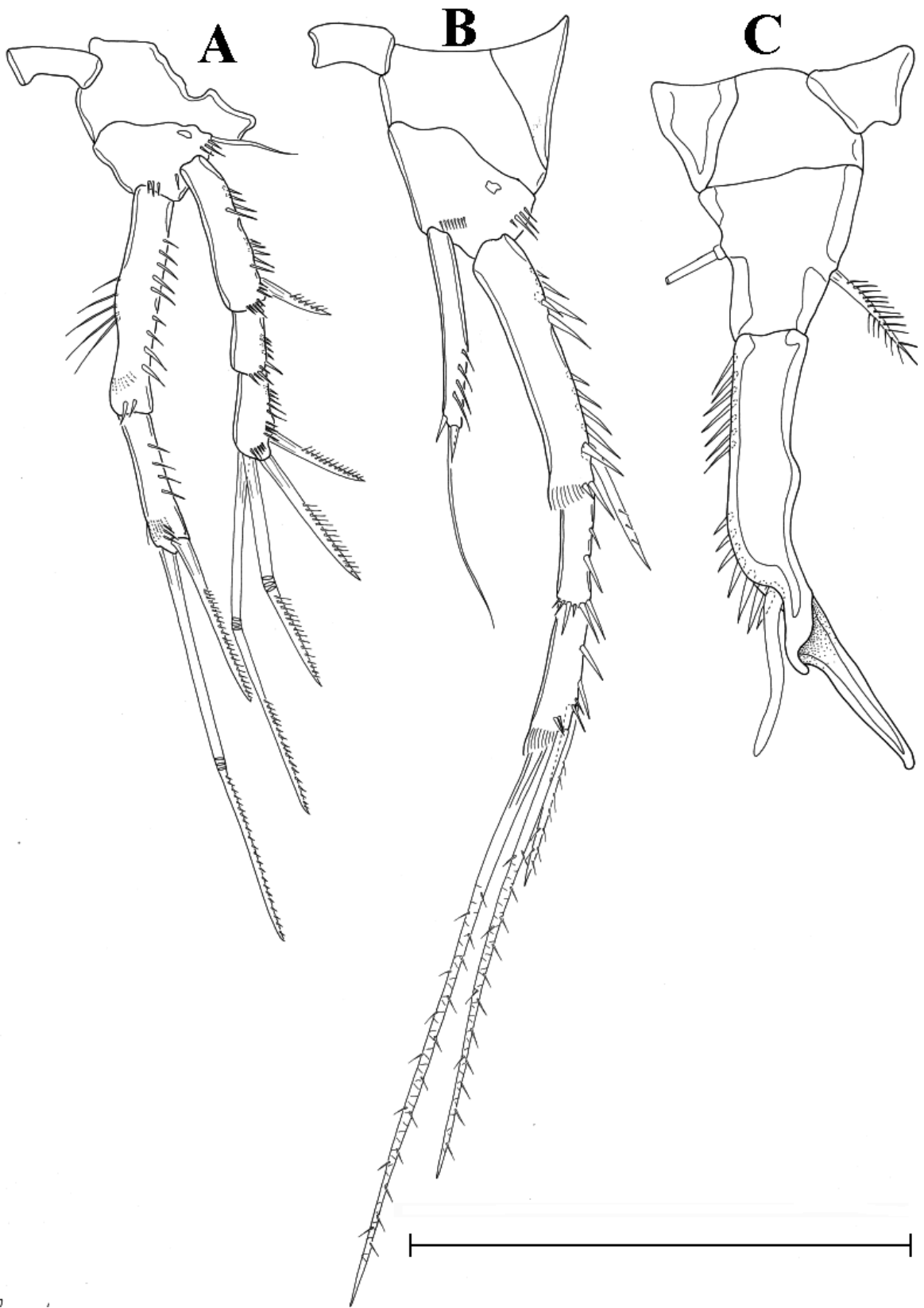


Figure 50- *Remaneicaris oncophora* (Noodt, 1965). Male; A, leg 1; B, leg 2; C, leg 3. Scale bar a= 25µm.

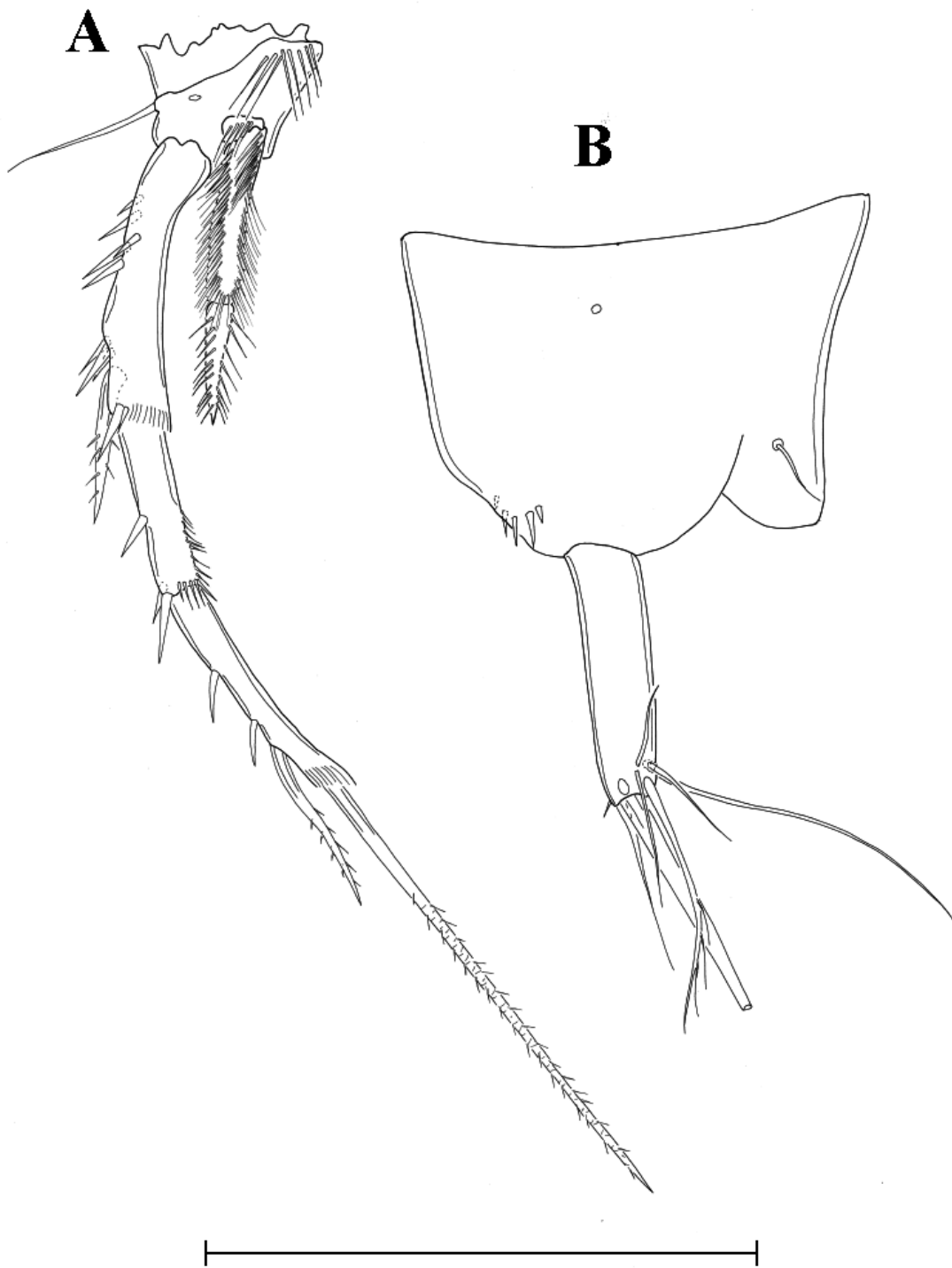


Figure 51- *Remaneicaris oncophora* (Noodt, 1965). Male; A, leg 4; B, telson in a lateral view. Scale bar a= 50 μ m.

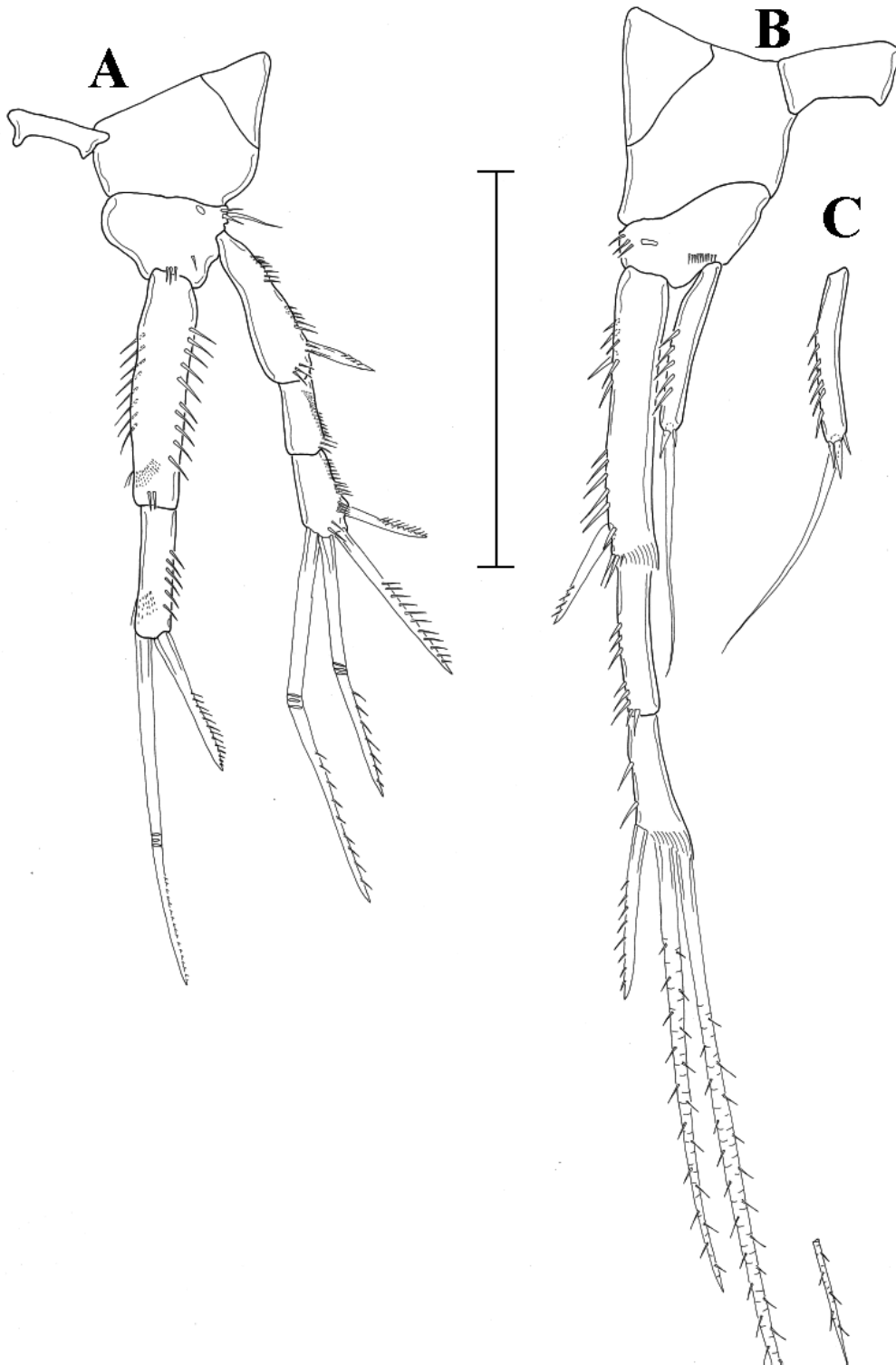


Figure 52- *Remaneicaris membranacea* (Noodt, 1965). Male; A, leg 1, B, leg 2. C, end of the leg 2 of female. Scale bar a= 50 μ m.

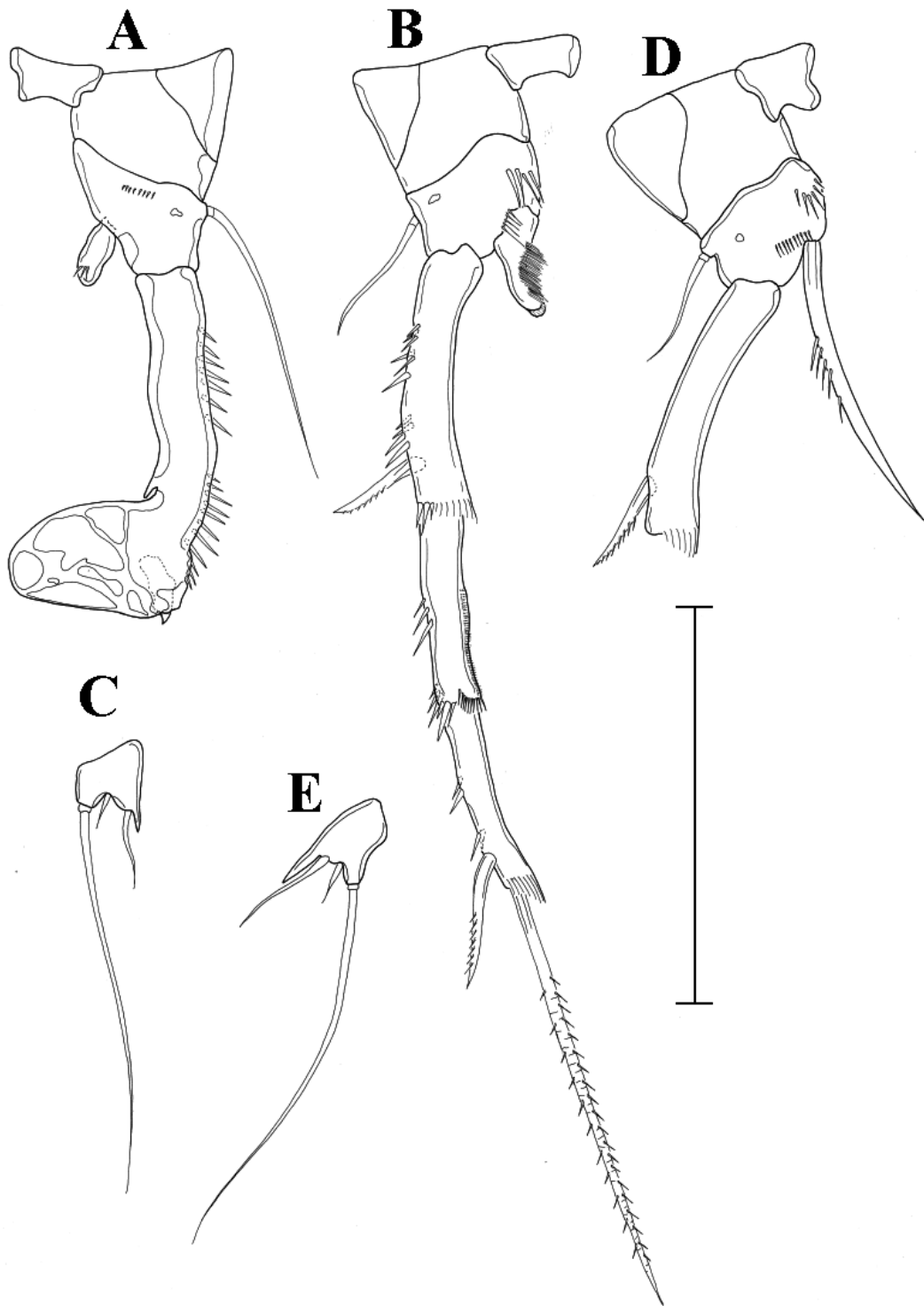


Figure 53- *Remaneicaris membranacea* (Noodt, 1965). Male; A, leg 3; B, leg 4; C, leg 5. Female; D, leg 4; E, leg 5. Scale bar a= 50 μ m.

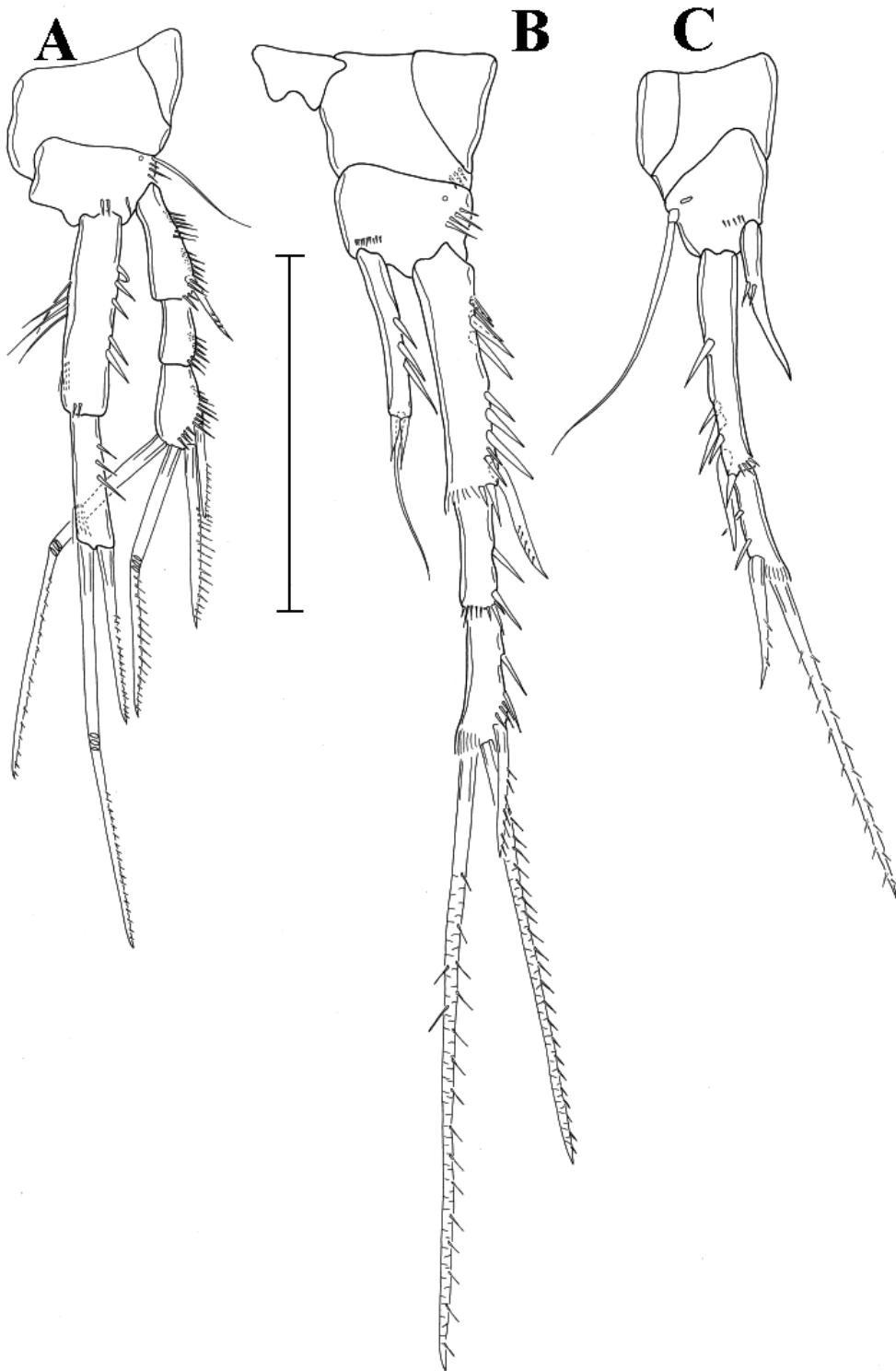


Figure 54- *Remaneicaris rhizophora* (Noodt, 1965). Female; A, leg 1; B, leg 2; C, leg 3. Scale bar a= 50 μ m.

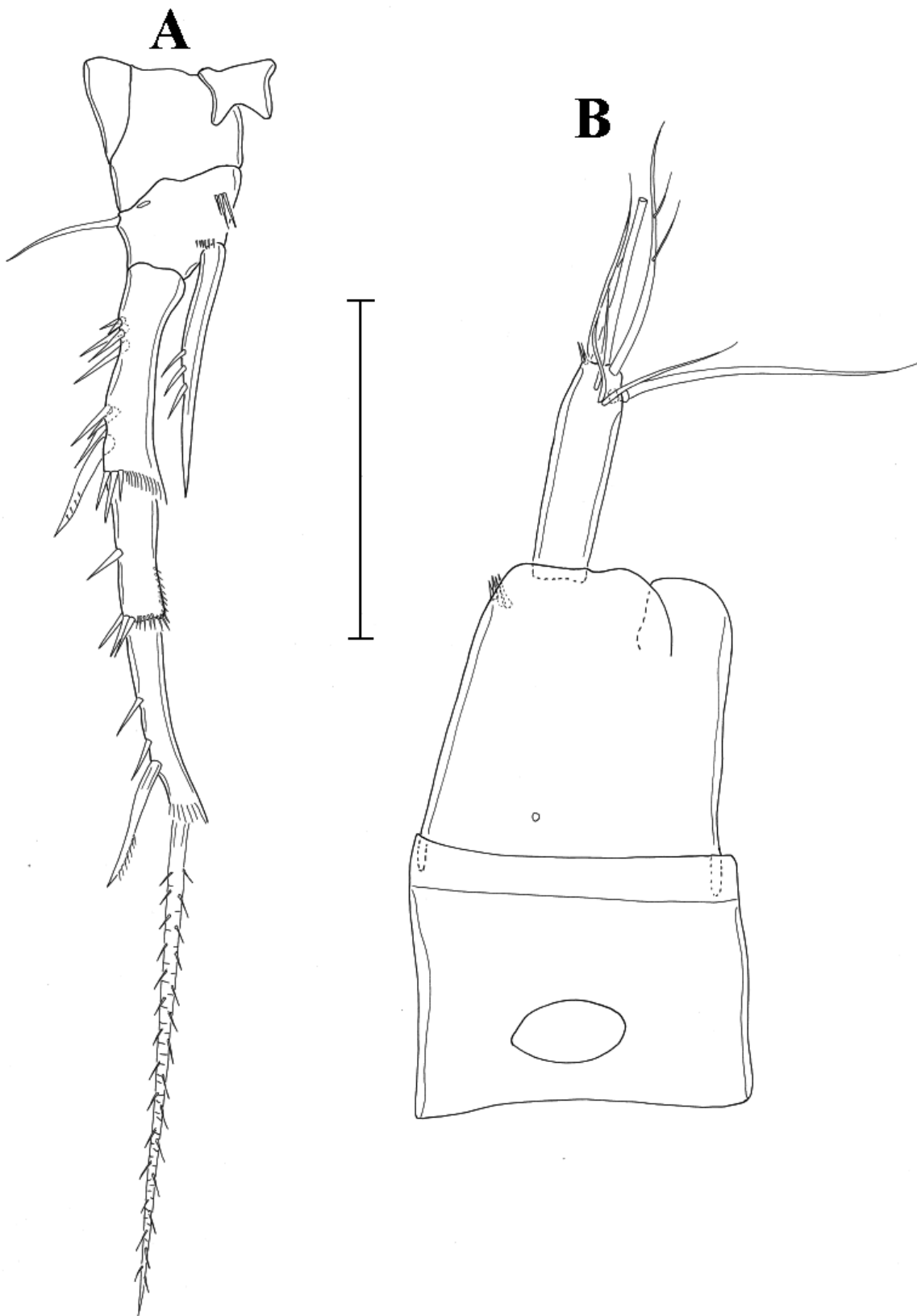


Figure 55- *Remaneicaris rhizophora* (Noodt, 1965). Female; A, leg 4; B, telson in a lateral view. Scale bar = 50 μ m.

Conclusion

The genus *Remaneicaris* is the most diverse and widely distributed group of parastenocaridids from the Neotropical region, occurring from the Central America until the Austral America.

This genus is clearly monophyletic, being easily identifiable due to the subdistal position of the outer spine of the third exopodite of the leg 4, absence of an intercoxal sclerite on the leg 5 and due to the presence of at least one long outer spine on the medial region of exopodites 2 and 3 of legs 2 and 4. Other species of parastenocaridids, such as *Parastenocaris spinosa* Wells, 1964 and *P. spinipes* Wells, 1964 from Africa and *P. Pusillus* Chappuis, 1954 and *P. trisaetosa* Chappuis, 1954 from Madagascar, also have a similar transformation regarding the position of the outer spine of the third exopodite of leg 4. However, these species are typical “Parastenocaridinae” and, thus, since *Remaneicaris* do not belongs to the “crown group” of this subfamily; it is more parsimonious to consider that the positioning of the subdistal spine on the African and Magascarian species as being result of convergent evolution.

Beyond some extremely derived characters such as the presence of lateral integumental windows in some urosomites (not present on the groundpattern of the genus), this genus can also be easily characterized due to the presence of an uncommon set of plesiomorphies never seen within the family. We can mention, for example, the presence of endopod on the leg 3 of males and two setae on the first endite of Mx2. In all other parastenocaridids, to our knowledge, the males' leg 3 does not have endopod and the first endite of Mx2 has only one seta.

Due to this, Corgosinho (chapter 5) propose that this genus should be considered the most basal group within the family Parastenocarididae, constituting an independent subfamily (viz.

Remaneicaridinae) that can be divided in at least five monophyletic groups of species (viz. *argentina*, *analuizae*, *tridactyla*, *persephone* and *cordobaensis*).

Following this idea, this genus could also be divided into smaller genera. However, in view of the scarcity of data about the diversity of this group on the Americas, a better option was to maintain the unity of *Remaneicaris*, until the acquisition of a better knowledge of the distribution and diversity of this mega genus. In the future, more studies should be conducted in some remote regions of the Central and South America, if one intend rise the monophyletic groups of *Remaneicaris* to the status of genera..

Additionally, more studies need to be done in other tropical regions (i.e. Sahara), given the possibility that *Parastenocaris ahaggarica* is a true *Remaneicaris*.

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