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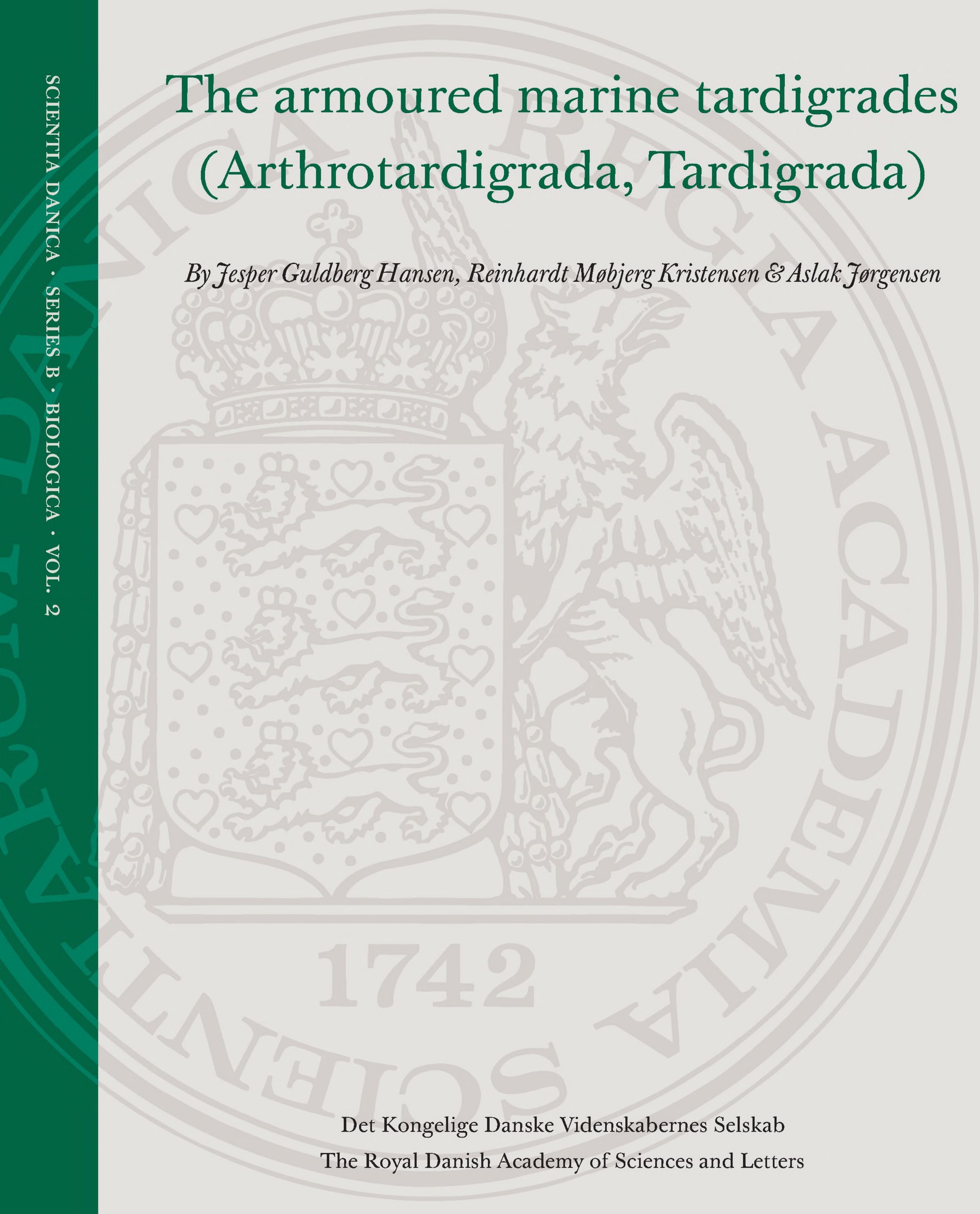
The armoured marine tardigrades (Arthrotardigrada, Tardigrada)

By Jesper Guldberg Hansen, Reinhardt Møbjerg Kristensen & Aslak Jørgensen



Det Kongelige Danske Videnskabernes Selskab
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Abstract

During the last three decades several new species of the marine stygarctid tardigrades have accumulated in the tardigrade collection at the Natural History Museum of Denmark, University of Copenhagen. The major aims of the present investigation were to describe some of the new species, to further increase the knowledge of the morphological diversity and to conduct phylogenetic analyses of all currently described species within the marine family Stygarctidae. The major objectives of the phylogenetic analyses were to investigate the internal phylogenetic relationships of Stygarctidae, their relationship to the most closely related previously recognized families (Neostygarctidae and Renaudarctidae), and the character evolution within the Stygarctidae. The outgroups were chosen to represent the extant members of presumed ancestral lineages of arthrotardigrades (*Coronarctus*, Coronarctidae and *Neoarctus*, Neoarctidae).

In order to evaluate the significance of the morphological diversity within the Stygarctidae, all species currently described have been personally examined by the authors and species new to science were described in each of the genera: *Faroestygarctus* nov. gen., *Mesostygarctus*, *Parastygarctus*, *Pseudostygarctus* and *Renaudarctus*. The character matrix consists of 31 species and 81 morphological characters. The characters have been scored from six main characters systems, i.e. the arrangement of head lobes, the cuticular segmental plates (head, body and caudal plates), the seminal receptacles, the legs and claws, the sense organs and the buccal apparatus. All 81 characters were parsimony informative and 51 are multistate characters.

The most notable results from the phylogenetic analyses are: 1) *Neostygarctus* is the sister-group to the previously known genera in Stygarctinae and is included in this subfamily; 2) *Faroestygarctus* nov. gen. is the sister-group to the other genera in Stygarctinae; 3) *Mesostygarctus* is a valid taxon and is the sister-group to *Pseudostygarctus*; 4) *Stygarctus spinifer* is the sister-group to the other *Stygarctus* species and is not a member of *Parastygarctus* as recently suggested.

In our opinion *Megastygarctides* is very different from the members of Stygarctinae and a position higher in the taxonomic hierarchy might be justified. Not surprisingly the Renaudarctidae is the sister-group to the Stygarctidae clade (Megastygarctidinae + Stygarctinae).

Key words: marine armoured tardigrades, new species, cladistics, phylogeny, evolution.

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Introduction

The phylum Tardigrada is constituted by microscopic metazoans related to either panarthropods (Arthropoda and Onychophora) or nematoidans (Nematoda and Nematomorpha) within the superclade Ecdysozoa (Dunn et al. 2008). Recently, tardigrades have received increased attention due to their adaptation to survival in extreme environments (reviewed in Møbjerg et al. 2011). Most of the described species of tardigrades are semi-terrestrial, however, the greatest morphological diversity is present within the marine arthrotardigrades.

Since the description of the first stygarctid *Stygarctus bradypus* Schulz, 1951, a further 19 species have been described in the family Stygarctidae. Representatives of this family are often a characteristic component in tidal and subtidal beach meiofaunas around the world. Following the monumental work by McKirdy et al. (1976) and several works by Renaud-Debyser (1965) and Renaud-Mornant (1970, 1979, 1981a and 1981b) most recent studies have been published by Italian investigators, who have significantly increased our knowledge of the diversity, ecology and systematics of these arthrotardigrades (De Zio Grimaldi et al. 1998; Gallo D'Addabbo et al. 2000 and 2001; Grimaldi de Zio et al. 1987).

The phylogeny has been investigated by Bello & Grimaldi de Zio (1998), who inferred the intergeneric relationships of the family. Kristensen & Higgins (1984) and Bello & Grimaldi de Zio (1998) regard Renaudarctidae as being the sister-group to Stygarctidae. Dewel & Dewel (1997), Renaud-Mornant (1982) and Simonetta & la Cave (1991) have argued for a position of the Stygarctidae close to the root of the tardigrade phylogenetic tree. *Stygarctus* was recently included in a phylogenetic study by Jørgensen et al. (2010) and its position was inferred to be near the base of the arthrotardigrades, however, the 28S rRNA sequence was somewhat aberrant with regard to the other arthrotardigrades.

Neostygarctus Grimaldi de Zio et al., 1982 was placed in Stygarctidae until Grimaldi de Zio et al. (1987) erected a new family, Neostygarctidae, for this monotypic genus. The phylogenetic position of *Neostygarctus* is of special interest as it resembles the members of Stygarctinae in general body outline. However, *Neostygarctus* exhibits cuticular extensions on the body and has unique claws, but these features might simply be autapomorphic features. Of special interest is the phylogenetic position of *Mesostygarctus intermedius* Renaud-Mornant, 1979 and *Stygarctus spinifer* Hiruta, 1985 within Stygarctidae; it has recently been proposed that these taxa be assigned to *Pseudostygarctus* and *Parastygarctus*, respectively (Gallo D'Addabbo et al. 2001). Two new species belonging to the genus *Megastygarctides* have recently been described (Hansen & Kristensen 2006). This study revealed several taxonomic important characters of the genus *Megastygarctides* not shared by any other members of the Stygarctidae.

The morphological difference between the two subfamilies of Stygarctidae (Stygarctinae and Megastygarctidinae) is pronounced, as is the variation within the different character systems. The plate and the sense organ character systems constitute approximately half the characters used in the data matrix for phylogenetic analyses. Furthermore, we introduce the seminal receptacles as a new character system, which shows a surprisingly high diversity within the Stygarctidae. The morphological diversity of the seminal receptacles has not been thoroughly studied in other arthrotardigrade families.

A Stygarctidae-like animal has been pictured as the ancestral tardigrade in recent paleontological studies on panarthropod evolution (Dewel & Dewel 1997; Budd 2001). The genus *Stygarctus* was used as one of the terminals in the strict consensus tree of Dewel and Dewel (Figure 10.5, 1997). In their phylogenetic analysis *Stygarctus* branches off between the extinct lobopodian *Aysheaia* and the extinct lateral-flapped *Kerygmachela*. These new paleontological analyses were not very different from the conclusions of older reports on the phylogeny of lobopods and tardigrades (Renaud-Mornant 1987; Simonetta & la Cave 1991). However, Renaud-Mornant (1987) argued that the genus *Parastygarctus* might resemble the stem group for all tardigrades. More recently, a minilobopod *Orstenotubulus evamuellerae* was described from the Cambrian Orsten Fauna (Maas et al. 2007). This new fossil has sensory structures and spines similar to those of stygarctids.

During the last three decades several undescribed species of stygarctids have accumulated in the tardigrade collection at the Zoological Museum, The Natural History Museum of Denmark, University of Copenhagen. Zwickl and Hillis (2002) argued that for enhancing phylogeny reconstruction it is more important to increase the number of taxa, than to increase the number of characters. Therefore, including these species into the phylogenetic analyses conducted in the present study was thus expected to increase the phylogenetic resolution at higher levels, particularly as a new genus (and subfamily) is described and new species are added to the former monotypic Renaudarctidae and *Mesostygarctus*.

The major aims of this investigation were to describe the new species, to further increase the knowledge of the morphological diversity, and to conduct phylogenetic analyses of all currently described species within the family Stygarctidae. The major objectives of the phylogenetic analyses are to investigate the phylogenetic relationships within Stygarctidae, the relationship to closely related families (Neostygarctidae and Renaudarctidae), the character evolution within the Stygarctidae and to discuss the characters in a phylogenetic framework.

Material and Methods

Taxon sampling

In the data matrix for the cladistic analysis the taxa are arranged according to the classification scheme suggested by Bello & Grimaldi de Zio (1998) (Table 1). The character matrix consists of 31 species and 81 morphological characters (See Table 11). The characters have been scored from six main characters systems, i.e., the arrangement of head lobes, the cuticular segmental plates (head, body and caudal plates), the seminal receptacles, the legs and claws, the sense organs and the buccal apparatus. All species currently described have been examined by the authors (Table 1). All 81 characters were parsimony informative, and 51 are multistate characters.

The ingroup, Stygarctidae, consists of 26 species. Stygarctinae (21 species) with genera *Mesostygarctus* Renaud-Mornant, 1979 (2), *Parastygarctus* Renaud-Debyser, 1965 (7), *Pseudostygarctus* McKirdy et al., 1976 (5), *Stygarctus* Schulz, 1951 (6) and *Faroestygarctus* nov. gen. (1), and Megastygarctidinae (5 species): *Megastygarctides* McKirdy et al., 1976 (5). The four outgroups are Renaudarctidae, *Renaudarctus* Kristensen & Higgins, 1984 (2), Neostygarctidae, *Neostygarctus* Grimaldi de Zio et al., 1982 (1), Neoarctidae, *Neoarctus* Grimaldi de Zio et al., 1992 (1) and Coronarctidae, *Coronarctus* Renaud-Mornant, 1974 (1) (see Table 2). The outgroups were chosen to represent presumed overall generalized arthrotardigrades (*Coronarctus* and *Neoarctus*) and arthrotardigrades (*Neostygarctus* and *Renaudarctus*) with a close phylogenetic relationship to Stygarctidae. The family Halechiniscidae has not been included as an outgroup as in Bello & Grimaldi de Zio (1998) because we regard it as more distantly related to Stygarctidae than *Neostygarctus* and *Renaudarctus*.

New species are described in each of the genera: *Renaudarctus*, *Faroestygarctus* nov. gen., *Mesostygarctus*, *Parastygarctus* and *Pseudostygarctus* (Table 2).

Sampling sites

Renaudarctus fossorius nov. sp. was collected in the intertidal zone in coarse carbonate sand at Gladstone, Tannum Sand, Queensland, Australia, in September, 1995 by R. M. Kristensen. *Faroestygarctus dezioae* nov. gen. et nov. sp. from the Faroe Bank was collected at 120 - 249 meter depth in coarse shell gravel with a small amount of organic matter (BIOFAR stations 573, 785 and 2013). For a thorough description of the locality refer to Nørrevang et al. (1994) and Hansen et al. (2001). *Mesostygarctus spiralis* nov. sp. was collected in the intertidal zone in carbonate sediment at the rocky shore of Nelson Park, Sidney Harbour, Australia in August, 1979 by N. Svennevig. *Parastygarctus svennevigi* nov. sp. and *Parastygarctus robustus* nov. sp. were collected in the tidal zone at 2 meter depth in coralline sand at Magdelaine Reef, North Cay, Australia in April 1979 by N. Svennevig. *Pseudostygarctus galloae* nov. sp. from Ras Al Tanajib, Arabian Gulf, Saudi Arabia, was collected in intertidal sandy sediment during the Northern Area Intertidal Sampling Program of ARAMCO in 1982 (see Hansen & Kristensen, 2006).

In addition to the type material listed below, we have examined new material of *Parastygarctus sterreri, Stygarctus bradypus* and *Stygarctus gourbaultae*. Specimens of *Parastygarctus sterreri* were found in coralline sand collected from Australia (Heron Island and Willis Island, Coral Sea), Bermuda (Castle Island and North Rock) and Florida (6 miles station and Pepper State Park). Specimens of *Stygarctus bradypus* were found in coralline sand collected from Saudi Arabia (Ras Al Tanajib, Arabian Gulf) and Hawaii (Kaluanuí Beach). Specimens of *Stygarctus gourbaultae* were found in coralline sand collected from Florida (Pepper State Park).

Table 1. Representation of all taxa included in the phylogenetic analysis. BA = buccal apparatus, SR = seminal receptacles, F = female, M = male, N = neotenic, L = larval stage known.

Outgroup	**Author, year**	**Sex**	**BA**	**SR**
Coronarctus	**Renaud-Mornant, 1974**			
Coronarctus verrucatus	Renaud-Mornant, 1987	F	x	x
Neoarctus	**Grimaldi de Zio et al., 1992**			
Neoarctus primigenius	Grimaldi de Zio et al., 1992	F	x	x
Neostygarctus	**Grimaldi de Zio et al., 1982**			
Neostygarctus acanthophorus	Grimaldi de Zio et al., 1982	F/M/L	x	x
Renaudarctus	**Kristensen & Higgins, 1984**			
Renaudarctus fossorius nov. sp.	Hansen et al., present account	F/M/L	x	x
Renaudarctus psammocryptus	Kristensen & Higgins, 1984	F/M	x	x

Ingroup				
***Faroestygarctus* nov. gen.**	**Hansen et al., present account**			
Faroestygarctus dezioae nov. sp.	Hansen et al., present account	N/F/L	x	x
Megastygarctides	**McKirdy et al., 1976**			
Megastygarctides isounguis	Renaud-Mornant, 1981	F	x	
Megastygarctides orbiculatus	McKirdy et al., 1976	F/M		(x)
Megastygarctides setoloso	Morgan & O'Reilly, 1988	M		
Megastygarctides christinae	Hansen & Kristensen, 2006	F/M		x
Megastygarctides gerdae	Hansen & Kristensen, 2006	F/M		x
Mesostygarctus	Renaud-Mornant, 1979			
Mesostygarctus intermedius	Renaud-Mornant, 1979	F/M/L	x	(x)
Mesostygarctus spiralis nov. sp.	Hansen et al., present account	F		x
Parastygarctus	**Renaud-Debyser, 1965**			
Parastygarctus biungulatus	Morone de Lucia et al., 1984	N/F/M		x
Parastygarctus higginsi	Renaud-Debyser, 1965	F/M	x	x

Parastygarctus mediterranicus	Gallo D'Addabbo et al., 2001	F/M/L		
Parastygarctus renaudae	Grimaldi de Zio et al., 1987	F/L	x	x
Parastygarctus robustus nov. sp.	Hansen et al., present account	F		x
Parastygarctus sterreri	Renaud-Mornant, 1970	F/M/L	x	x
Parastygarctus svennevigi nov. sp.	Hansen et al., present account	F/M	x	x
Pseudostygarctus	**McKirdy et al., 1976**			
Pseudostygarctus apuliae	Gallo D'Addabbo et al., 2000	F		x
Pseudostygarctus galloae nov. sp.	Hansen et al., present account	N/F/L		x
Pseudostygarctus mirabilis	de Zio Grimaldi et al., 1998	F/M	(x)	x
Pseudostygarctus rugosus	Gallo D'Addabbo et al., 2001	M/L		
Pseudostygarctus triungulatus	McKirdy et al., 1976	F/M/L		(x)
Stygarctus	**Schulz, 1951**			
Stygarctus abornatus	McKirdy et al., 1976	F/M	(x)	
Stygarctus bradypus	Schulz, 1951	F/M/L	x	(x)
Stygarctus gourbaultae	Renaud-Mornant, 1981	F/M	x	x
Stygarctus granulatus	Pollock, 1970	F/M/L	x	x
Stygarctus lambertii	Grimaldi de Zio et al., 1987	F/M/L		x
Stygarctus spinifer	Hiruta, 1985	F/M		x

Table 2. Overview of number and sex of studied specimens of the new species described in the present study.

Species	**Locality**	**Number and sex**
Renaudarctus fossorius nov. sp.	Australia	2 females, 1 male, 1 larva
Faroestygarctus dezioae nov. gen. et nov. sp.	Faroe Islands	6 females, 1 larva
Mesostygarctus spiralis nov. sp.	Australia	1 female
Parastygarctus robustus nov. sp.	Australia	6 females
Parastygarctus svennevigi nov. sp.	Australia	2 females, 4 males
Pseudostygarctus galloae nov. sp.	Saudi Arabia	6 females, 1 larva

Material examined

The type material of *Renaudarctus psammocryptus, Megastygarctides orbiculatus, Pseudostygarctus triungulatus, Stygarctus abornatus* and *Stygarctus granulatus* together with paratypes of *Parastygarctus higginsi* and *Stygarctus gourbaultae*, was obtained through a loan from the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C. The type material of *Neoarctus primigenius, Neostygarctus acanthophorus, Parastygarctus biungulatus, Parastygarctus mediterranicus, Parastygarctus renaudae, Pseudostygarctus apuliae, Pseudostygarctus mirabilis, Pseudostygarctus rugosus*, and *Stygarctus lambertii* as well as specimens of *Mesostygarctus intermedius*, *Parastygarctus sterreri* and *Stygarctus bradypus*, was studied during a visit to the Department of Zoology, University of Bari, Italy. The type material of *Megastygarctides isounguis* and *Mesostygarctus intermedius* was obtained through a loan from the National Museum of Natural History, Paris, France. The holotype of *Megastygarctides setoloso* was obtained through a loan from the National Museums of Scotland, Edinburgh, Scotland and the type material of *Stygarctus spinifer* from the Zoological Institute, Faculty of Science, Hokkaido University of Education, Japan. The type material of *Megastygarctides christinae*, *Megastygarctides gerdae* and *Coronarctus verrucatus* is deposited in the collection of the Zoological Museum, SNM, University of Copenhagen, Denmark.

Light (LM) and scanning electron microscopy (SEM)

Tardigrades were released from the sediment by freshwater shocking, retained in a 32 µm mesh net and fixed in 4% buffered formaldehyde. The specimens prepared for LM were mounted on microslides in glycerol or EPON-embedded and studied using phase-contrast and Nomarski-technique microscopy. All microslides were afterwards sealed with Glyceel®. Micrographs of the specimens were taken on an Olympus BX51 microscope with an Olympus C-3030 zoom digital camera. All drawings were made using a camera lucida. The specimen prepared for SEM was dehydrated in an ethanol/acetone series prior to critical point drying (see Jørgensen & Kristensen 2001). The dried specimen was mounted on an aluminium stub and coated with palladium for observation in a JEOL JSM-6335-F SEM.

Phylogenetic Analysis

Maximum parsimony (MP; cladistic) and Bayesian inference (BI) methods were used in phylogenetic reconstruction. The parsimony analyses were conducted in PAUP* version 4.0b10 (Swofford 2001) and the Bayesian inference in MrBayes3.1 (Huelsenbeck & Ronquist 2001). The two different optimality criteria (MP and BI) were chosen to examine the robustness of the inferred phylogenies through comparison of topologies and nodal support.

The maximum parsimony analyses were performed using the heuristic algorithm with starting trees obtained using the random addition sequence settings and tree-bisection-reconnection (TBR) branch-swapping of 1000 replicates. All 81 characters were unordered. Different weighting or taxon removal schemes were explored 1) unweighted; 2) successive weighting of the data matrix using the rescaled consistency index (RC). The RC index is the product of the consistency index (CI, measures the amount of homoplasy) and the retention index (RI, measures the amount of synapomorphic similarity) (Farris 1989). The CI, RI and RC indices are presented in table 9; 3) analyses with either *Coronarctus* or *Neoarctus* (or both) removed using *Renaudarctus* as the single outgroup.

Bootstrap-resampling analyses with 1000 replicates were conducted to assess the relative support for internal nodes. The following percentages have been used to specify the bootstrap support < 50% = unsupported, 50-69% = low support, 70-89% = intermediate support and 90-100% = high bootstrap support.

Bremer support (Decay index) (Bremer 1988) was calculated using MacClade 4.03 (Maddison & Maddison 2001) and PAUP*. The significance of the phylogenetic relationship between the major clades was tested using the Kishino-Hasegawa (KH) test implemented in PAUP* (Kishino & Hasegawa 1989). The evolution of the characters was investigated using character tracing implemented in MacClade 4.03.

The following three phylogenetic relationships were tested statistically (their branch length compared to the shortest tree from the unweighted parsimony analysis) using Kishino-Hasegawa tests in PAUP*: 1) *Stygarctus spinifer* as the basal taxon of *Parastygarctus*, in order to test the possibility of *S. spinifer* belonging to a *Parastygarctus* as proposed by Gallo D'Addabbo et al. (2001). 2) The *Mesostygarctus* clade as an unresolved basal part of *Pseudostygarctus*, in order to test the possibility of *Mesostygarctus* being synonymous with *Pseudostygarctus* as proposed by Gallo D'Addabbo et al. (2001). 3) A monophyletic Stygarctidae (Stygarctinae + Megastygarctidinae) with *Neostygarctus* as the sister-group. The Kishino-Hasegawa test was originally designed to evaluate topologies specified *a priori*; the evaluation of *a posteriori*-specified trees is a violation of the test and may result in severely biased results (Goldman et al. 2000; Shimodaira & Hasegawa 1999). However, as proposed by Hipp et al. (2004), we used the parsimony-based KH-test in PAUP* in the absence of an implemented likelihood model for morphological data. Since the investigated tree topologies were compared to the most-parsimonious tree the *P* values were converted to modify the analysis to a one-sided test (Goldman et al. 2000; Buckley et al. 2001). Significant differences between the two trees being compared should be considered with caution for the above mentioned reasons.

The Bayesian inference of the morphological character matrix was performed based on the gamma-shaped rate variation. Metropolis-coupled Markov chain Monte Carlo simulations (MCMC) were run with four chains using the random tree option for 1,000,000 generations, and Markov chains were sampled at intervals of 100 generations. A burn-in of 1000 trees as assessed by the log probability plateau was removed and a 50% majority rule consensus tree with the clades posterior probabilities was created (MrBayes3.1; Huelsenbeck & Ronquist 2001). Phylogenetic inference was repeated three times to assess congruence. It has been shown that Bayesian posterior probabilities give a very high estimation of node reliability, unlike maximum parsimony bootstrap values which are more conservative (see Douady et al. 2003). The posterior probabilities represent P values, and P ≥ 95% was considered evidence of significant support (Huelsenbeck & Ronquist 2001), which corresponds to the high bootstrap support (90-100%).

Terminology

Most of the terminology is standard and known to those familiar with arthrotardigrade morphology. However, since we introduce a large amount of new information, especially on the morphology of the cuticular plates, our interpretation of these characters and its consequences for terminology is summarised in the following section to facilitate the reading. Furthermore, we include three species in our investigation which exhibit larval characters in adulthood, suggesting a paedomorphic origin of these taxa. Currently, however, the concept of paedomorphic species is not clearly defined; Gould (2000) aptly stated that "The burgeoning literature of heterochrony has, in the past decade, become fatally confused by a logical error in widely adopted proposals for an expanded terminology." In order to prevent any potential confusion or misinterpretation, we provide an outline of our adoption/interpretation of the terminology used in postembryonic development and paedomorphosis.

Morphology

Segmental plates: The plate covering the head is called the cephalic plate, the first three trunk plates are called body plates I-III, and the fourth trunk plate is called the caudal plate.

Intersegmental plates: The plate between the cephalic plate and body plate I is called intersegmental plate I, the plate between body plates I and II and between body plates II and III is called intersegmental plates II and III, respectively. The plate between body plate III and the caudal plate is called intersegmental plate IV. In some species of *Parastygarctus*, *Pseudostygarctus* and *Stygarctus*, it can be difficult to determine the nature of the space between two segmental plates, as it lacks any prominent lateral margins. In previous literature, only the medial thickening of the space between two segmental plates has been interpreted as an intersegmental plate. However, after examining all currently described stygarctid species, we have come to the conclusion that the medial thickening of the cuticle of some intersegmental plates must be considered as cuticular sculptures.

Intersegmental ridges: In species of *Renaudarctus* and *Megastygarctides*, a prominent cuticular structure, forming a ridge rather than a true plate, is present between segmental and intersegmental plates.

Sheets: The term "sheet" refers to a thin epicuticular membrane or lamella present in species of *Stygarctus*, *Mesostygarctus* and *Pseudostygarctus*.

Postembryonic development and larval characters

In heterotardigrades, there are successive moults between hatching and sexual maturity. In this way the animal, through a series of juvenile instars/stages, reaches its sexual maturity and definitive habitus. The lack of the anal and genital pore in the early series of moults distinguishes this developmental period as a true larval stage, thus the postembryonic development in heterotardigrades is indirect. In a thorough review, Bertolani et al. (1984) conclude that the postembryonic development in heterotardigrades, although with some exceptions, conforms to a general scheme. They suggested dividing the larval stage into three age classes; two age classes whose most evident features were the number of digits or claws and the absence/presence of an anal and genital pore. A third age class completes the larval stage before the animal finally reaches its definitive habitus.

During the first age class, the larva lacks both anus and gonopore and generally has two less digits or claws on each leg than the adult. This first larval age is probably of short duration and ends with the first moult.

In the second age class, the larva has an anus and the same number of digits or claws as the adult but lacks the gonopore (exceptionally it is incipient). The larva may go through several moults (juvenile instars) during this stage, which is also characterized by a complete, or almost complete, lack of fundamental reproductive structures.

The third age class is characterized by the presence of anus, completely developed gonopore, and definitive number of claws or digits. This habitus is probably characteristic of the greater part of the life cycle and includes not only somatic growth but also maturation of the gonad. In some cases, third age class instars display species-specific modification or the appearance of cuticular structures which are not present in adults. In the absence of such structures it is not always possible to distinguish between sexually immature individuals (third age class) and adults that have just oviposited.

Only few studies on the postembryonic development in Arthrotardigrada have been performed (Renaud-Mornant & Anselme-Moizan, 1969; Kristensen, 1978; Renaud-Mornant, 1984; Renaud-Mornant, 1989). Additional information on variations in features during ontogenesis has mostly been supplied in species descriptions, in which superficial observations on a single larval/instar type (typically the "two-clawed" and/or "four-clawed" larva) are included. While primary larval characters, such as smaller number of digits or claws and the absence/presence of an anal and genital pore, are common to most heterotardigrades and relatively easy to recognize, the assignment of secondary larval characters is less defined. In Stygarctidae however, modifications to the shapes of the dorsal cuticular plates, lateral processes, head lobes and cephalic sense organs occur during ontogenesis thus providing reliable information on secondary larval character states. While being largely constant within each genus, these larval character states show no general trend throughout the Stygarctidae and the assignment of secondary larval character states, on the basis of inter-generic comparisons should be conducted with caution.

Heterochrony

In *Ontogeny and phylogeny*, Gould (1977) reviewed the history of the concept of heterochrony and proposed a streamlined terminology for various kinds of heterochrony. In the glossary of the book Gould (1977) defined heterochrony as: "phyletic onset or timing of development, so that the appearance or rate of development of a feature in a descendent ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny." When the evolutionary change results in the retention of juvenile characters into adult life, it is called paedomorphosis. Different modes of change in rates and timing may use different terminology for the results, i.e., progenesis for paedomorphosis by accelerated sexual maturation, and neoteny for paedomorphosis by delayed somatic maturation. In practise, heterochrony is almost always studied as change in the relative timing of events in two related taxa, as true ancestral-descendent comparisons are rarely available. Although Gould's treatment of heterochrony was enormously influential on the way the concept is used today, his approach was restricted to changes in developmental events characterized by size and shape parameters. Later authors consider Gould's approach to heterochrony (called de Beerian heterochrony by Raff & Wray, 1989 or growth heterochrony by Smith, 2001) too limited as a general way to view changes in timing of development, thus an expanding terminology of heterochrony has been subject to numerous and widely adopted proposals (for recent reviews see McNamara, 1997, Klingenberg, 1998, Hall, 1999, McKinney, 1999, Gould, 2000, Smith, 2001). However, as it is beyond the scope of our investigation to include parameters other than size and shape, and have followed the concept of heterochrony as defined by Gould (1977).

Neoteny as the result of paedomorphosis has been suggested for only a few species of arthrotardigrades, namely *Tanarctus heterodactylus* Renaud-Mornant, 1980, *Tholoarctus natans* Kristensen & Renaud-Mornant, 1983, *Parastygarctus biungulatus* Morone De Lucia, Grimaldi de Zio & D'Addabbo Gallo, 1984, and the two *Styraconyx* species, *S. nanoqsunguak* Kristensen & Higgins, 1984 and *S. qivitoq* Kristensen & Higgins, 1984. In *Tanarctus heterodactylus*, the external digits are much shorter than the internal digits. Renaud-Mornant (1980) interpreted the short external digits as being less developed and therefore considered this feature an indication of neoteny or, in other words, she nominated the short external digits as a larval character retained by delayed somatic maturation. If this were true and following Gould's (1977) concept of paedomorphosis, it should be possible to trace similar ontogenic features in closely related taxa. However, currently there is no data supporting the character of short external digits in either closely related taxa or other arthrotardigrade taxa during ontogenesis. Thus, *Tanarctus heterodactylus* does not represent the most obvious case of neoteny. In *Tholoarctus natans*, *Styraconyx nanoqsunguak* and *S. qivitoq*, a special kind of instar (dwarf male) occurs during ontogenesis (Kristensen & Higgins, 1984). This instar reaches sexual maturity while still displaying simple external claws, which are considered a larval character, and therefore appears a clear case of neoteny. However, in the series of juvenile instars of *S. qivitoq*, a sexually immature instar occurs (fourth instar), possessing fully developed external claws, thus questioning the sequence of events during ontogenic development. By suggesting that, "the male can mature after the second instar (dwarf male) or after the fourth instar, which is more usual" (Kristensen & Higgins, 1984), the authors contradict their own hypothesis of neoteny. The suggested sequence implies that dwarf males are the result of paedomorphosis by accelerated sexual maturation (progenesis) rather than by delayed somatic maturation (neoteny). However, both explanations are the result of paedomorphosis, so we consider this particular confusion of terminology less important. It is more important to define "adult life" or "adulthood" when accepting Gould's definition of paedomorphosis: "When the evolutionary change results in the retention of juvenile characters into adult life, it is called paedomorphosis". In the particular case of *S. qivitoq*, the postembryonic development of males and females might not be parallel. Another highly plausible explanation, to the observation of Kristensen & Higgins (1984), would be that the male reaches sexual maturity after the second instar (dwarf male) and its definitive habitus after a further moult, whereas the female reaches both sexual maturity and definitive habitus after the fourth instar. Thus the development of males includes at least four instars; both the first and second instars are two-clawed without a gonopore, the third instar is four-clawed with simple external claws and with a fully developed gonopore (sexually mature) and the fourth instar possess both fully developed three-pointed claws and gonopore. The development of females includes at least five instars; the first and second instars are two-clawed without a gonopore, the third instar is four-clawed with simple external claws and lacking a gonopore, the fourth instar with three-pointed claws still without a gonopore. The fifth instar is an adult. If "adult life" is then defined as being the definitive habitus, neither adult males nor adult females of *S. qivitoq* display juvenile characters. Without the retention of juvenile characters into adult life, there are no clear indications of paedomorphosis. It is more likely that the reproductive strategies of males and females are different. However, further studies on the postembryonic development and reproductive strategies of these species are needed to answer these questions with more certainty. A more obvious case of paedomorphosis is presented by *Parastygarctus biungulatus*. This species possesses only two claws on each leg in adults; this is generally accepted as a primary larval character. As there are no other clear detectable larval characters retained in adults of this species, *P. biungulatus* is considered as neotenic. Noda (1993) later identified another two clawed adult *Parastygarctus* species from Japanese waters. Although it was never described, it suggests that neoteny is prevalent among species of *Parastygarctus*.

Summary: In view of the above considerations, paedomorphosis (in arthrotardigrades) is not as prevalent as previously suggested and can only be ascribed to *Parastygarctus biungulatus* (and *Parastygarctus* nov. sp. from Japan). Even with the addition of two new paedomorphic species described in the present study, paedomorphosis remains restricted to stygarctid species.

Abbreviations

an	anus
ap	apophysis
bpI-III	dorsal body plates I-III
cap	caudal plate
cb	genital cuticular bar
cep	cephalic plate
cE	cirrus E
cf	longitudinal cuticular folds
cg	claw gland
co	constriction of posterior process
cp	caudal process
cs	cuticular sculpture (of the cephalic plate, dorsal body plates and intersegmental plates)
csp	caudal spike
du	duct of seminal receptacles
ec	external cirrus
fu	stylet furca
go	gonopore
gp	genital cuticular pocket
gr	genital ring
gu	midgut
hp	process of the lateral head lobe
ic	internal cirrus
ipI-IV	intersegmental plate 1-4
irI-IV	intersegmental ridges 1-4
lc	lateral cirrus
leI-IV	leg I-IV
lpI-IV	leg plate I-IV
ma	muscle attachment
mc	median cirrus
mo	mouth cone
op	opening of seminal receptacle duct
ov	ovary
pa	anterior lateral process of body plate
pb	pharyngeal bulb
pc	primary clava
pd	dorsal posterior process
ph	accessory plate of the head
pl	placoid
pp	posterior lateral process of body plate
pv	ventral posterior process
ro	rosette cell
rs	seminal receptacle
sc	secondary clava
se4	sense organ of leg IV
sef	frontal sense organ
sep	tongue-shaped sense organ plate
sh	sheet
sp	posterior spine of the lateral head lobe
st	stylet
vh	ventral head plate
vp	ventral plate
vpI-IV	ventral plate of body segment 1-4

Taxonomic descriptions

Family Renaudarctidae Kristensen & Higgins, 1984

Diagnosis (emended). Arthrotardigrades with segmental dorsal and ventral plates, both claws and toes present. Four toes are accompanied by four accessory claw spines on each foot in the adults. Primary and secondary clavae, and complete set of cephalic cirri present.

Genus *Renaudarctus* Kristensen & Higgins, 1984

Diagnosis (emended). Renaudarctidae with segmental dorsal plates, two dorsal intersegmental plates, four dorsal intersegmental ridges, a dorsal plate on each leg, and thin ventral plates. Each body plate with a pair of lateral spines. Caudal plate with two pairs of lateral spikes, one pair of caudal spikes, and lateral margins continuous with furca-like caudal extensions. Complete set of cephalic sense organs. Leg IV with small ovoid papilla; all other legs lack sensory structures. Cirrus E with cirrophore. Female and male with ovoid gonopore papillae adjacent to terminal anal system. Female with latero-ventral projections containing seminal receptacles.

Type species: *Renaudarctus psammocryptus* Kristensen & Higgins, 1984.

Renaudarctus fossorius nov. sp. (Figures 1-4, Table 3)

Diagnosis. Typical dorsal plate pattern of the genus: head plate, three body plates, caudal plate, two intersegmental plates, four intersegmental ridges and a dorsal plate on each leg. Five paired ventral plates present. One pair of large and highly complex cephalic sensory structures flanking the mouth cone, consisting of three fused components; a frontal sense organ, the secondary clava and a large tongue-shaped sensory plate. The secondary clava is a bulbous projection, not bent around the external cirrus. Cirrus E with cirrophore. Lateral lobes of the three-lobed anal system enlarged. Female and male with ovoid gonopore papillae in contact with terminal anal system. Female with latero-ventral projections containing seminal receptacles. Accessory genital vesicle associated with the seminal receptacle is lacking.

Material – Holotype, female [ZMUC TAR 721], allotype, male [ZMUC TAR 722] and 2 paratypes [ZMUC TAR 723-724] collected 23 September, 1995 at Gladstone, Tannum Sand, Queensland, Australia (23°56' S; 151°22' E) by R.M. Kristensen.
Depth range – Intertidal, at 50 to 110 cm sediment depth.
Sediment type – Coarse carbonate sand.
Etymology – From the Latin word: *fossorius*, meaning "adapted to digging".

Holotype: The holotypic female (Figures 1, 2, and 4) is 92 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle (Figure 2) forms seven plates: head plate, three body plates, caudal plate, and two intersegmental plates. Each of the three body plates extends laterally into a pair of posteriorly curved acute processes (Figure 2). The second body plate has a broad and bell-shaped bulge at the dorsal midline. The third body plate has an indistinct median furrow. The caudal plate has two pairs of lateral processes, and a single pair of caudal spikes. The anteriormost lateral processes of the caudal plate are posteriorly curved, similar to the processes of the body plates, although much smaller. The posteriormost lateral processes of the caudal plate are dome-shaped. The caudal spikes are triangular acute processes situated on a furca-like caudal extension which is continuous with the lateral margin of the caudal plate. The intersegmental dorsal plates between first and second body plate and between second and third body plate both appear sub-divided, having a median furrow or suture. The cephalic segment is separated from the first trunk segment by a

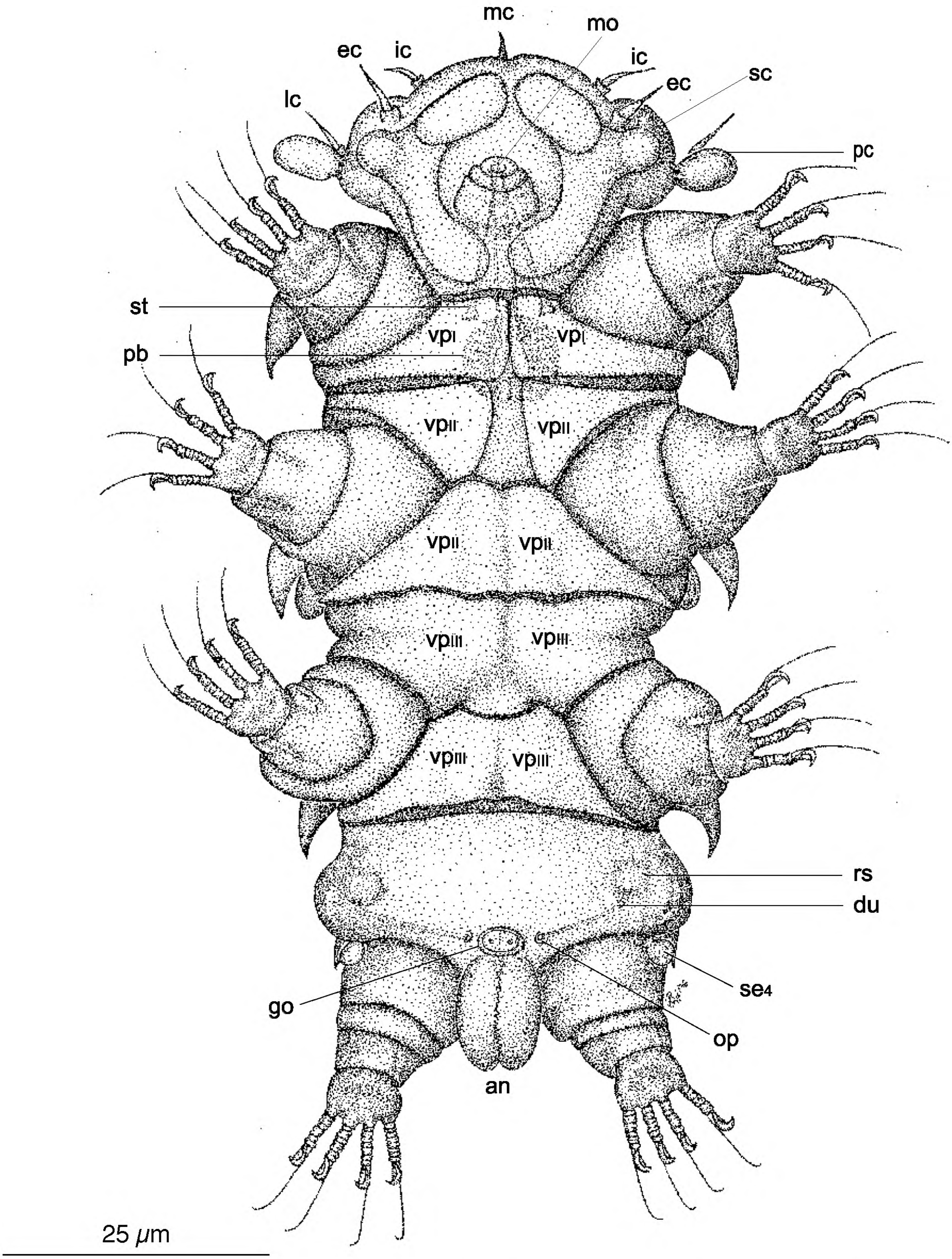

Figure 1. *Renaudarctus fossorius* nov. sp.: adult holotypic female, ventral view. Drawing by Birgitte Rubæk.

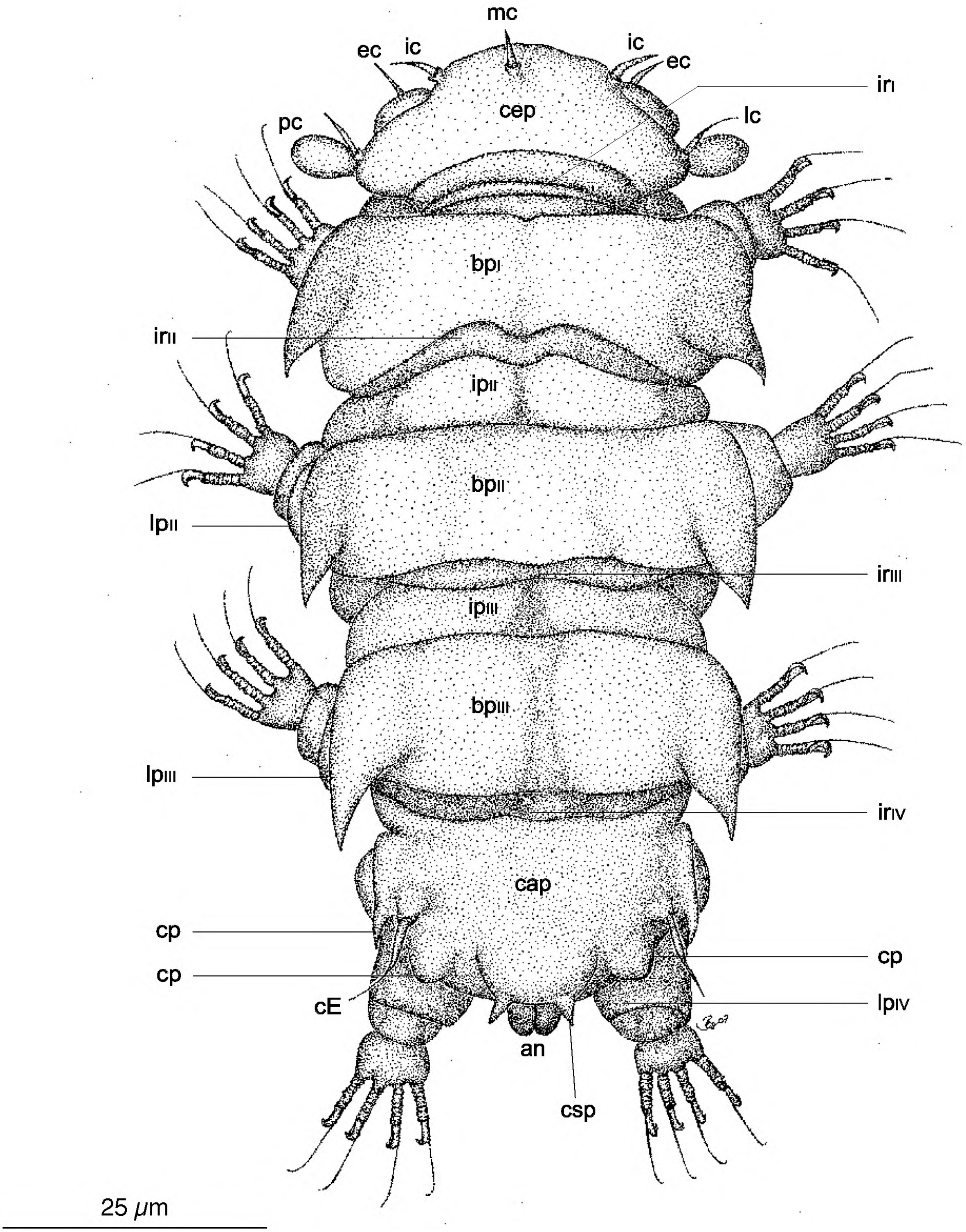

Figure 2. *Renaudarctus fossorius* nov. sp.: adult holotypic female, dorsal view. Drawing by Birgitte Rubæk.

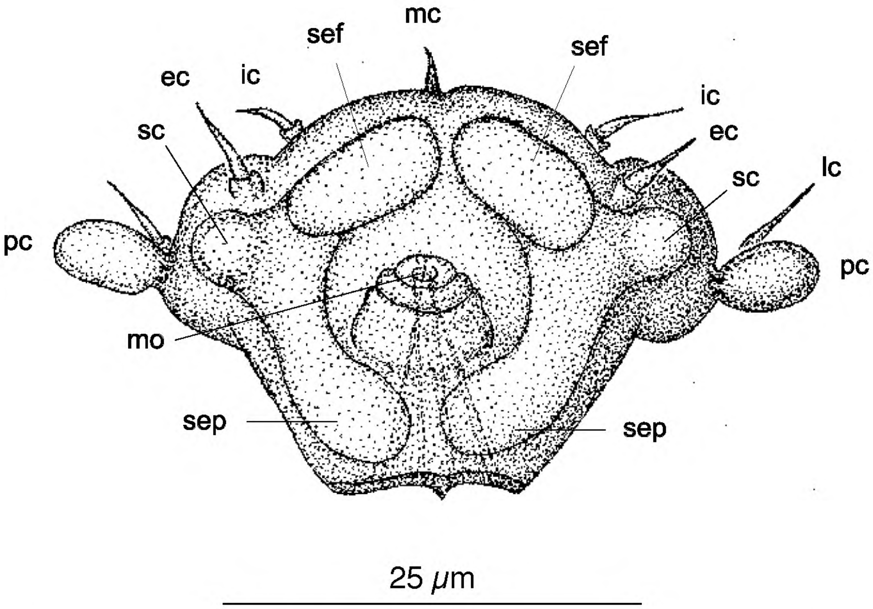

Figure 3. *Renaudarctus fossorius* nov. sp.: Close-up on the head of the holotypic female, ventral view. Drawing by Birgitte Rubæk.

Table 3. Morphometric summary of the specimens of *Renaudarctus fossorius* nov. sp. examined and measured in LM. Measurements in µm.

ZMUC no	Holotype female TAR 721	Allotype male TAR 722	Paratype female TAR 723	Mean	St.dev.	n	Range	Paratype juvenile TAR 724
Body length	92	102	110	101,3	9,0	3	92-110	62
Buccal tube	14	–	–			1	14	–
Pharyngeal bulb	9	–	–			1	9	–
Stylet	15	–	–			1	15	–
Median cirrus	5	4	6	5,0	1,0	3	4-6	3
Internal cirri	6	6	6	6,0	0,0	3	6	5
External cirri	6	5	7	6,0	1,0	3	5-7	6
Lateral cirri	7	7	7	7,0	0,0	3	7	8
Primary clavae	6	6	6	6,0	0,0	3	6	4
Secondary clavae								
(width x height)	5 x 4	6 x 3	-			2		4 x 2
Cirri E	11	14	13	12,7	1,5	3	11-14	11
4th leg sense organ	3	4	4	3,7	0,6	3	3-4	2

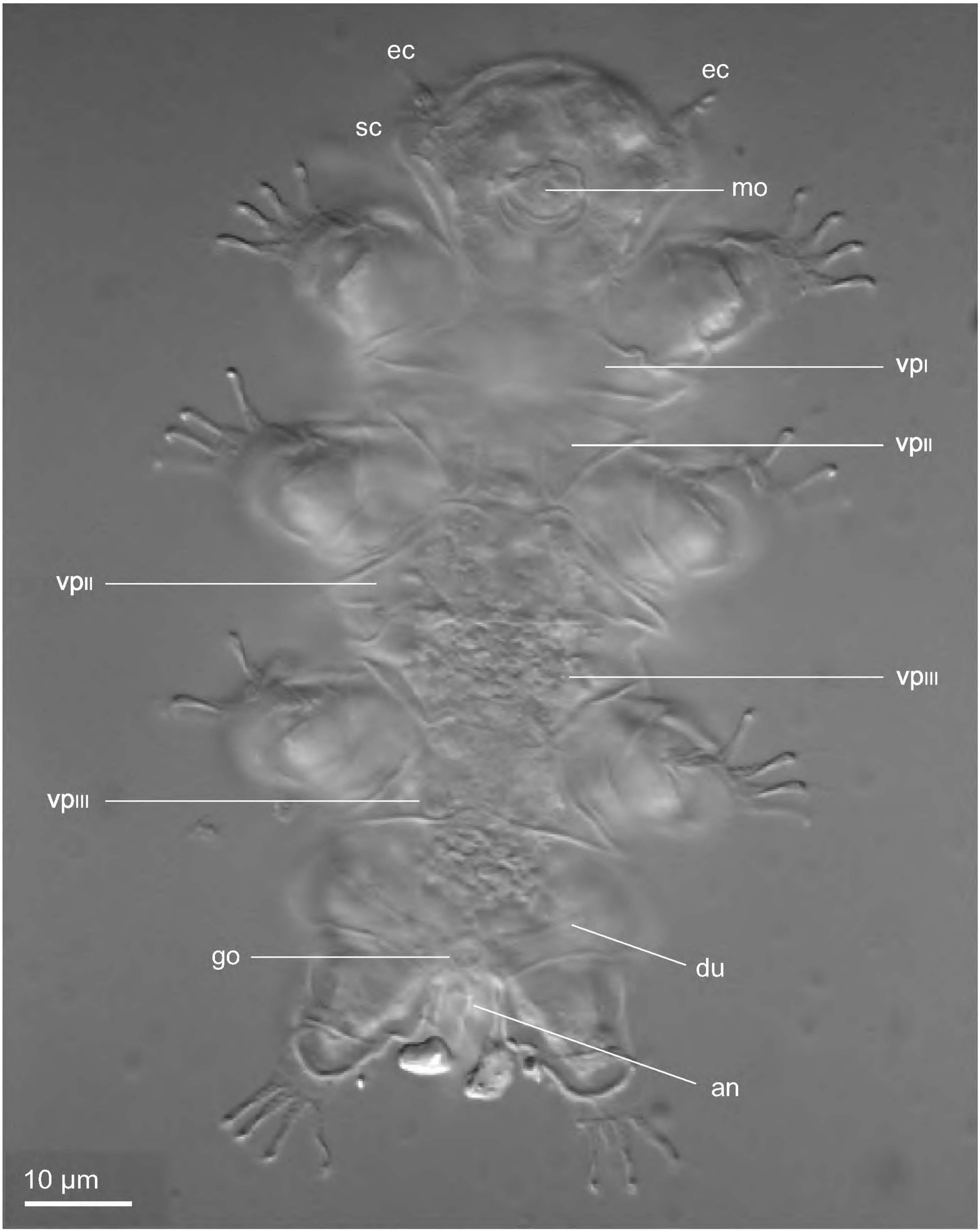

Figure 4. DIC-micrograph of *Renaudarctus fossorius* nov. sp., holotypic female.

prominent intersegmental ridge, and three more ridges separate the next three trunk segments. All legs have a small dorsal plate on the femur. A single pair of ventral plates is present posteriorly on the first trunk segment, whereas two pairs, an anterior pair and a posterior pair, are present on both second and third trunk segment (Figure 1).

The compact head is inserted on the body without any neck extension. A complete set of cephalic sense organs is present (Figure 3). Primary clava and lateral cirrus are inserted separately arising from the lateral margin of the head. The lateral cirrus (7 µm) is inserted dorsal to the primary clava. The primary clava is small and oval (6 µm). Two large and highly complex sensory structures flank the mouth cone, occupying almost the entire ventral surface of the head. Each of these structures consists of three fused components; a frontal sense organ, the secondary clava and a large tongue-shaped sensory plate (Figure 3). The frontal sense organ is slightly oval, almost rectangular structure very similar to the frontal sense organ of *Renaudarctus psammocryptus*. The secondary clava (4 µm x 5 µm) is a bulbous projection, inserted slightly posterior to the external cirrus. The large tongue-shaped sensory plate extends posteriorly, curving towards the ventral mid-plane, and ending posterior to the mouth cone. Like in *R. psammocryptus*, a small sense organ surrounds the mouth cone. All the cephalic cirri consist of a well-developed cirrophore, scapus and flagellum. Internal cirri (6 µm) are inserted ventrally, very close to the lateral margin of the frontal part of the cephalic plate. The external cirri (6 µm) are inserted frontally on the edge of the cephalic plate. The median cirrus (5 µm) arises dorsally, close to the edge of the frontal part of the cephalic plate. The cirrus E (11 µm) is inserted dorso-laterally on the caudal plate, without a pedestal. It consists of a bell-shaped cirrophore, an accordion-like scapus and a thin flagellum. The sense organ on the fourth leg (3 µm) is a spherical papilla inserted ventro-laterally on the first coxal segment (Figure 1).

The legs appear stumpy and weakly telescopic, with well defined coxa, femur, tibia and tarsus. From the hand-shaped tarsus, four wrinkled toes arise, each bearing a claw consisting of a strongly cuticularized portion and a thin, more translucent laminar portion. The transition between claw and toe is not clearly delineated. All claws have a thin accessory filament or spine.

The mouth opening is ventral and situated on a small cone. The pharyngeal apparatus (Figure 1) consists of a buccal tube (14 µm), pharyngeal bulb (9 µm) and stylets (15 µm). Each stylet is very thin with large furca, and stylet supports are absent. The pharyngeal bulb is situated posterior in the first trunk segment and has three short but very robust placoids. From the pharyngeal bulb, a short oesophagus leads to the diverticulated mid-gut. The anus (Figure 1 and 4) is a serrated slit surrounded by two large lateral lobes which protrude from the animal so that a portion can be seen in dorsal view (Figure 2). The caudal (third) lobe is reduced.

The reproductive system of the holotype female consists of a single ovary bearing one large ovum occupying most of the third trunk segment. The gonopore system consists of a simple oval papilla anteriorly adjacent to the anus (Figure 1 and 4). The two cuticular seminal receptacles are formed as small globular vesicles situated inside the ventro-lateral processes of the caudal plate. No accessory genital vesicles are present. The genital ducts are long, almost straight and open to the exterior laterally to the gonopore. As in *R. psammocryptus*, a small internal septum divides the gonopore (Figure 1).

The two-clawed larva is 62 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle is already differentiated into seven recognizable plates: head plate, three body plates, caudal plate, and two intersegmental plates. Intersegmental ridges are also present. Unfortunately, the larva is orientated in a way that makes any precise interpretation of the shape of preserved plates and ridges difficult. No lateral processes can be recognized on the body plates, thus the determination of their absence or presence, awaits the finding of further larval specimens. The caudal plate has not yet developed any lateral processes or caudal spikes; however a furca-like caudal extension, which is continuous with the lateral margin of the caudal plate, is present mid-dorsally. All legs have a small dorsal plate on the femur. Ventral plates are absent. A complete set of well-developed sense organs is present, including the cephalic sensory complex as seen in the adult. All the legs have two claws with long thin accessory filaments. Neither anus nor gonopore are present.

Remarks: *Renaudarctus fossorius* nov. sp. shares with *R. psammocryptus* the dorsal plate pattern, the presence of dorsal leg plates, the presence of ventral plates, the morphology of claws and toes, and the morphology of gonopore and anus. Thus, the new species confirms the diagnostic characters for the genus, set by Kristensen & Higgins, 1984. The most important differences between *R. fossorius* and *R. psammocryptus* are the shape of the secondary clava and the associated sensory complex, the number and size of the ventral plates, and the accessory genital vesicle. In *R. psammocryptus* the secondary clava is nearly sausage-shaped and bent around the base of the external cirrus, whereas in *R. fossorius* it is a bulbous projection, fused anteriorly with the frontal sense organ and posteriorly with a large, tongue-shaped sensory plate. In *R. psammocryptus* there are three pairs of small ventral plates: two pairs on the second trunk segment and a single pair on the third trunk segment. In *R. fossorius* there are five pairs of ventral plates: a single pair on the first trunk segment, two pairs on the second trunk segment and two pairs on the third trunk segment. Finally, the accessory genital vesicle associated with the seminal receptacles in *R. psammocryptus* is not present in *R. fossorius*, and the lateral anal lobes of the anal system are enlarged in *R. fossorius*.

Zoogeographical notes: Until this study the family Renaudarctidae had remained monotypic. The type species *Renaudarctus psammocryptus* was originally described from Pepper State Park, Fort Pierce and Red Reef Park, Florida. In both localities the specimens were found at 70-100 cm depth close to the mean low-water level in coarse carbonate sediment consisting of shell hash. The collections were made in 1982-1983. Unpublished data from Pollock and Higgins indicate that this species had already been collected in 1980 from Cap Hatien, Republic of Haiti and Monte Criste, Dominican Republic. Later in 1984 Renaud-Mornant (1984) published records of the species from Martinique and Guadeloupe (Antilles).

Noda (1994) published a brief account of two species of renaudarctids from Ryukyu Archipelago, Japan, and showed drawings of what he called *Renaudarctus psammocryptus* and gen. (?) sp. The latter had only two digits on leg IV. However, Noda (1994) could not describe the new genus from the single specimen he had found. The coralline sandy sediments were collected at the shallow depth of 15 cm in the mid intertidal zone. Noda (1994) stated that the occurrence of *R. psammocryptus* from Western Pacific far from the type locality (the East coast of North America) suggests that this species has a worldwide distribution.

From 13th August 1995 to 14th June 1996 an Australian Biological Research Study was carried out along the entire Eastern coast of Australia. About 80 marine localities were investigated. *Renaudarctus fossorius* was found at only one locality, Tannum Sand, Gladstone, Queensland, which was visited on three occasions. All specimens were found in shell hash at mean high-water level at a sediment depth ranging from 50 cm to 110 cm, close to the subsoil water.

During the 16-28 March 2005 collection of marine tardigrades for molecular data at Praslin and Mahé, Seychelles several beaches were investigated. A species of *Renaudarctus* was found at only Beau Vallon, Mahé in carbonate sand 100-130 cm depth in the sediment close to the mean low-water level. Our investigations using light microscopy and SEM show that this Indian Ocean species is very close to *R. psammocryptus*. Gallo et al. (2007) also reported the presence of *R. psammocryptus* and *Renaudarctus* sp. from the Seychelles.

Our zoogeographical conclusion is that the genus *Renaudarctus* has a worldwide distribution; however it has a very cryptic occurrence often found very deep in the carbonate sediment close to the freshwater subsoil water. In all localities the species is very rare.

Family Stygarctidae Schulz, 1951

Diagnosis. Arthrotardigrada with dorsal cuticle forming five dorsal plates: a cephalic plate, three body plates (segmental plates I, II and III), and a caudal plate (segmental plate IV); dorsal plates sometimes absent; head subdivided into lobes; intersegmental dorsal plates and ventral plates may be present. Complete set of cephalic cirri and two pairs of clavae. Stylet supports always absent. Legs non-digitate with four, three or two claws; claws with or without dorsal spurs or long dorsal filaments; claws attached with dorsal basal membrane. Leg sense organs present only on the fourth pair of legs. Sense organs on the fourth pair of legs as bulb-shaped papillae. Seminal receptacles formed as cuticular pouches with short straight ducts or with long sinuous ducts close to the gonopore.

Faroestygarctus nov. gen.

Diagnosis. Stygarctinae with perfectly semicircular head plate divided into three lobes: an anterior lobe bearing the median cirrus, internal cirri, external cirri and secondary clavae, and two posterolateral lobes bearing the primary clavae and lateral cirri. Three body plates, each with a pair of lateral processes tapering to flexible spines. Intersegmental dorsal plate present between second and third body plate. Caudal plate with a pair of ventro-lateral triangular processes. The primary clavae are small and oval. The secondary clavae are semi-globular. Dorsally inserted cirrus E with indistinct basal accordion articulation. Each leg with two claws with dorsal spurs. Seminal receptacles formed as small ventro-lateral spheroid vesicles with long sinuous ducts.

Etymology – The genus name is formed from a combination of the name of the type locality (the Faroe Bank) and the Greek words *stygos* "hate" and *arctos* "bear".

Type species: *Faroestygarctus dezioae* nov. sp.

Faroestygarctus dezioae nov. sp. (Figures 5-8 and 26, Table 4)

Diagnosis. As for the genus.

Material – Holotype, female [ZMUC TAR 715] and 1 paratype [ZMUC TAR 716] from BIOFAR station 2013 (61°00' N; 08°13' W), 2 paratypes [ZMUC TAR 717-718] from BIOFAR station 573 (61°12' N; 08°25' W) and 2 paratypes [ZMUC TAR 719-720] from BIOFAR station 785 (61°17' N; 08°32' W). Collected by R.M. Kristensen.
Type locality – Faroe Bank, Faroe Islands, North Atlantic Sea, BIOFAR station 2013. (61°00' N; 08°13' W) 19 September, 1998 at 120 m depth.
Depth range – 120-249 m.
Sediment type – gravel, coarse shell gravel, shell sand.
Etymology – To honour Prof. Susanna de Zio Grimaldi for her life long contribution to the knowledge of marine tardigrades.

Holotype: The holotypic female (Figures 5, 7A, B, D and 26) is 88 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle forms six plates: head plate, three body plates, caudal plate, and intersegmental plate III. Each of the three body plates extends laterally into a pair of acute processes, terminating in long flexible spines (Figure 8A). A single intersegmental plate is present, located between the second and third body plate. The posterior part of the caudal plate has a pair of ventro-lateral triangular processes. Ventral plates are absent. The dorsal cuticle is sculptured with a fine hexagonal pattern with an overlying network of thin cuticular ridges (Figure 8).

The head plate is perfectly semicircular (Figures 7C and 8B) without any deep indentations. A pair of internal and highly refractive cuticular funnel-shaped structures are present between the internal and external cirri (Figure 7A, B). They extend from the ventral side all the way through the head to the dorsal side. A complete set of well-developed cephalic sense organs are present. Primary clava and lateral cirrus are inser-

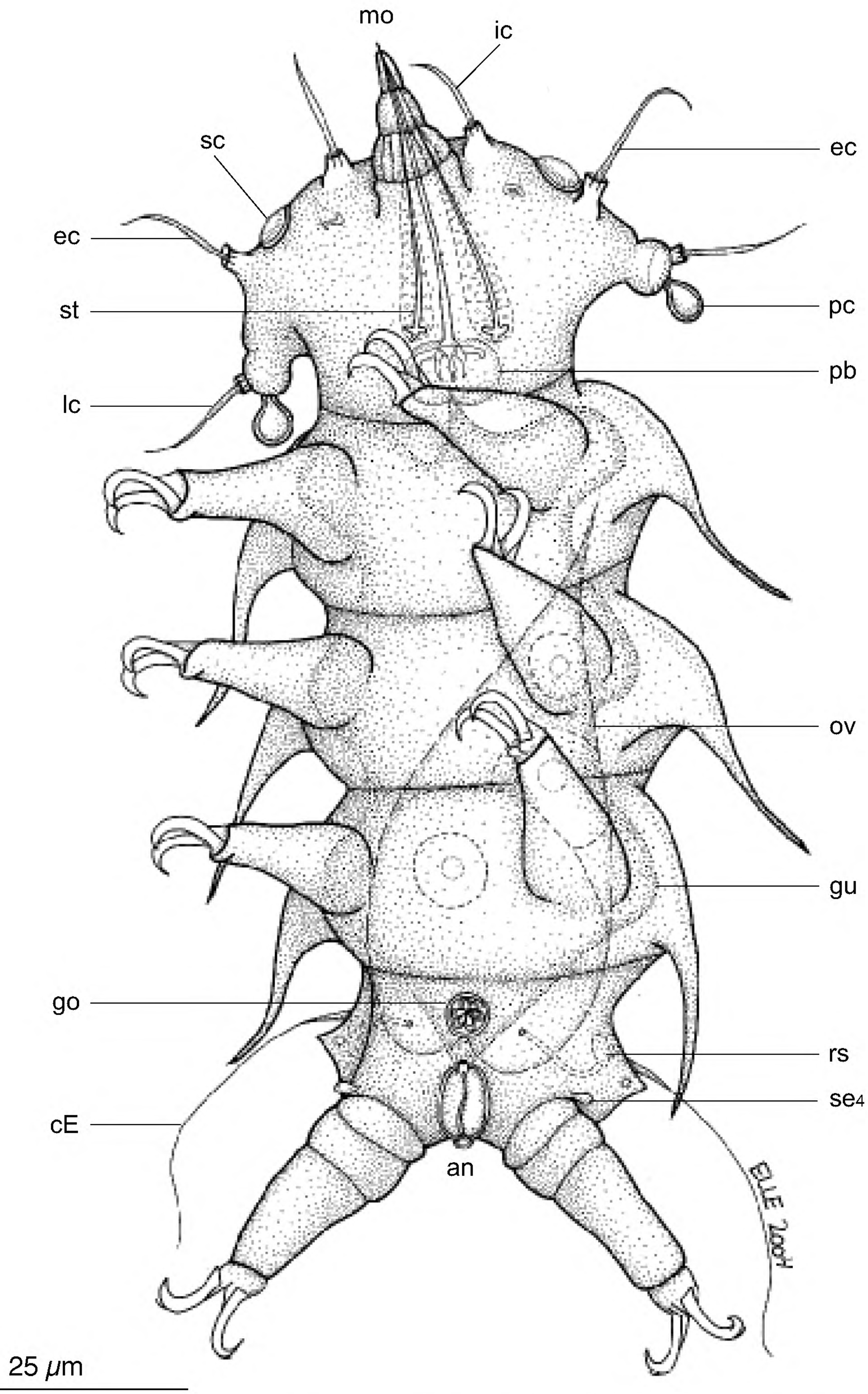

Figure 5. *Faroestygarctus dezioae* nov. sp.: adult holotypic female, ventral view. Drawing by Stine B. Elle.

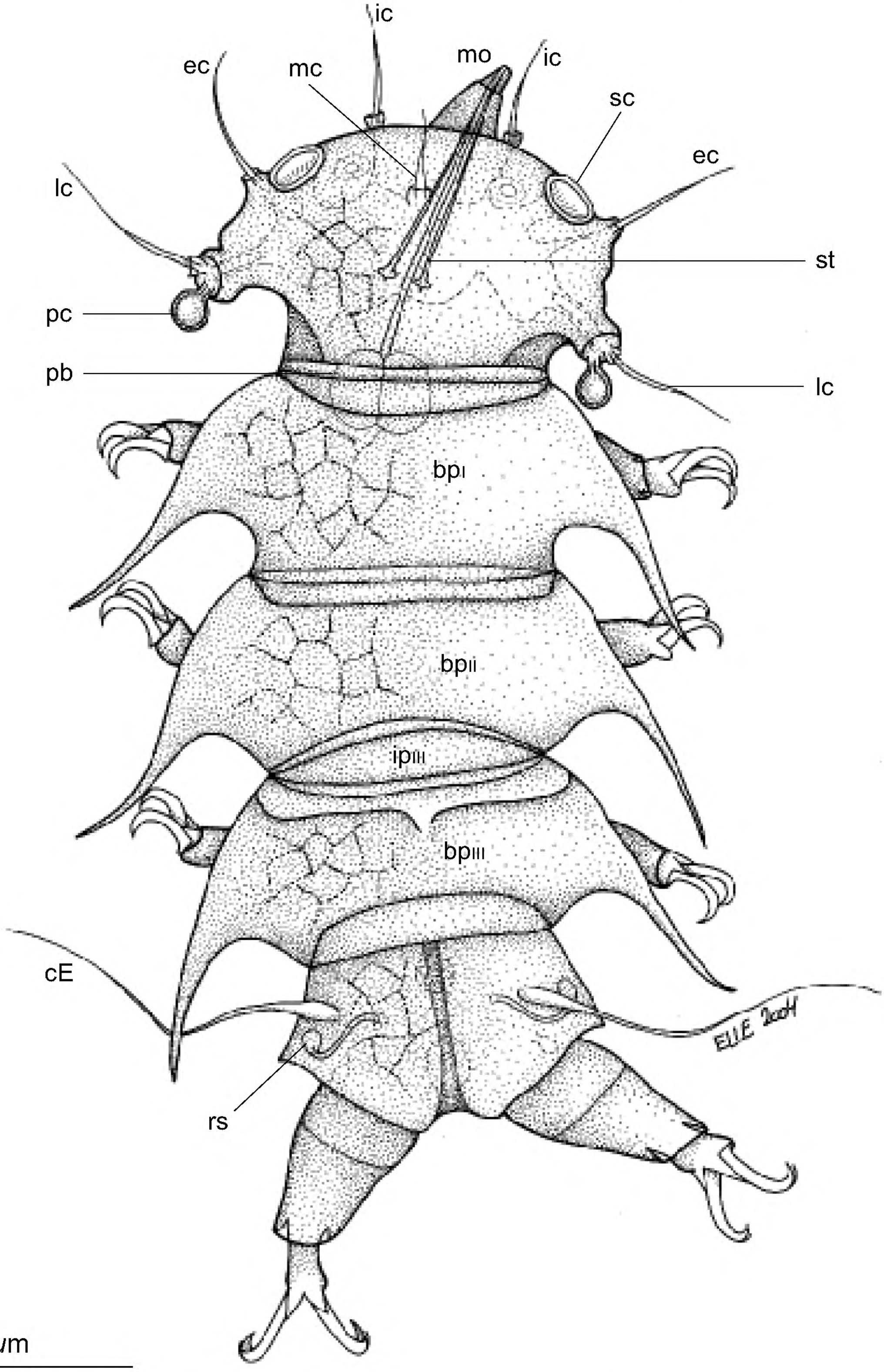

Figure 6. *Faroestygarctus dezioae* nov. sp.: adult paratypic female, dorsal view. Drawing by Stine B. Elle.

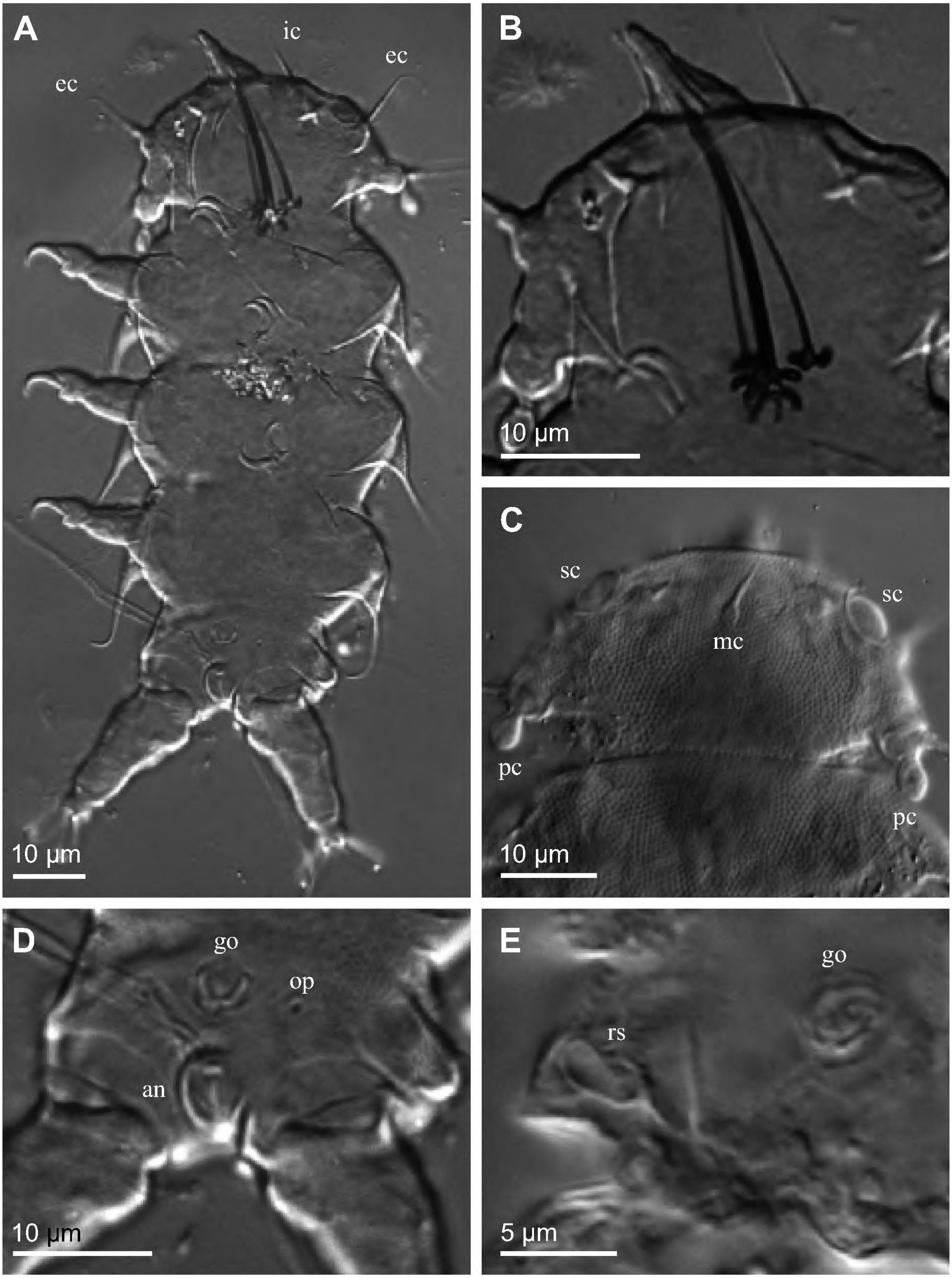
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Figure 7. DIC-micrographs of *Faroestygarctus dezioae* nov. sp. A. Ventral overview. B. Detail of the bucco-pharyngeal apparatus. C. Detail of the head, dorsal view, note the evident pillars in the cuticle. D. Detail of the caudal end. E. Detail of the gonopore and seminal receptacle.

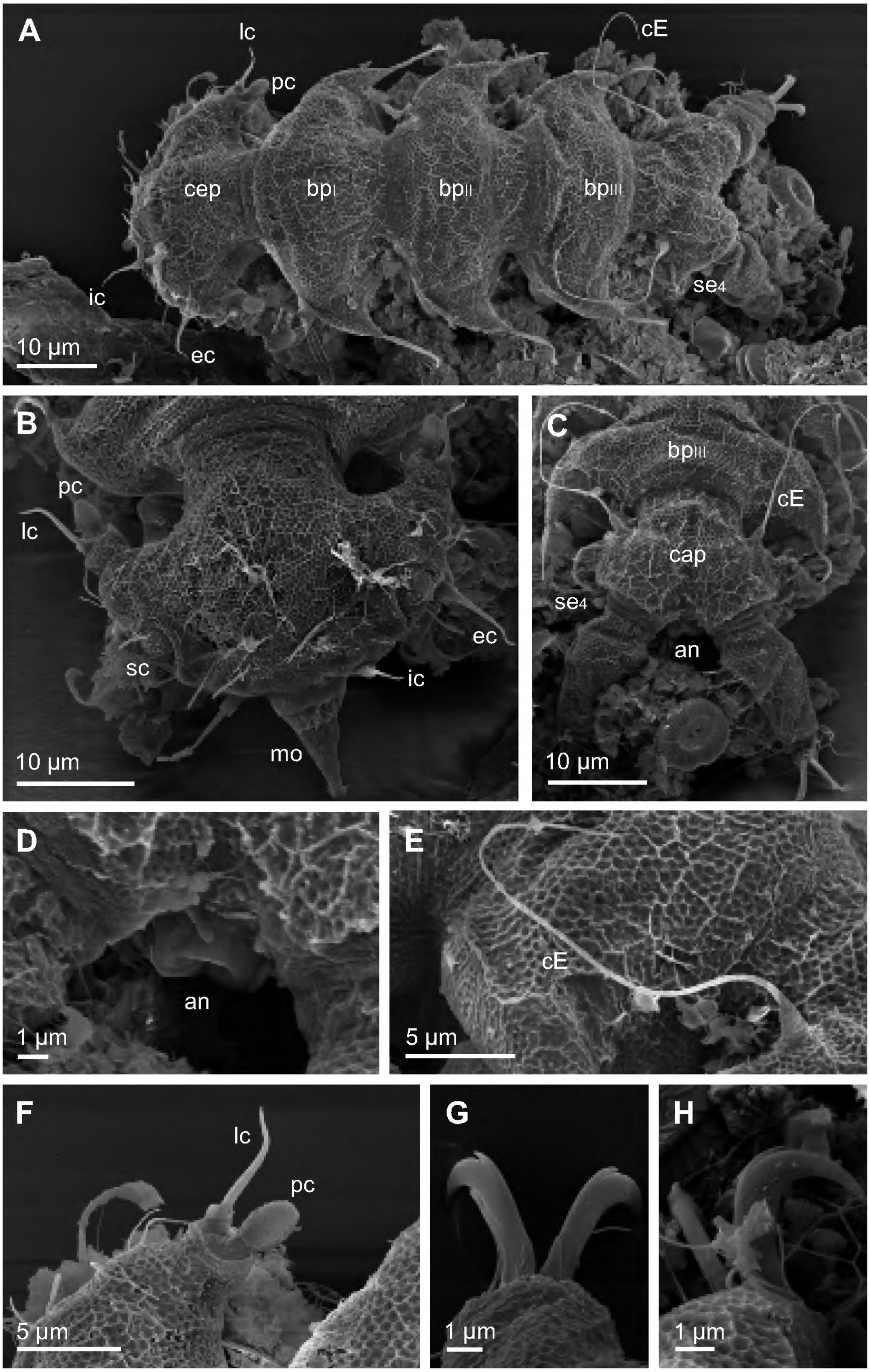


Figure 8. SEM-micrographs of *Faroestygarctus dezioae* nov. sp. A. Dorsal overview. B. Detail of the head. C. Detail of the caudal end. D. Anus. E. Detail of cirrus E, note the sculpture of the dorsal cuticle. F. Detail of on the lateral head lobe. G.-H. Claws of leg IV.

Table 4. Morphometric summary of the specimens of *Faroestygarctus dezioae* nov. sp. examined and measured in LM. Measurements in µm.

ZMUC no	Holotype female TAR 715	Paratype female TAR 716	Paratype female TAR 717	Paratype female TAR 718	Paratype female TAR 719	Mean	St.dev.	n	Range	Paratype juvenile TAR 720
Body length	88	88	87	-	81	86,0	3,4	4	81-88	55
Buccal tube	26	28	-	-	22			3	22-28	-
Pharyngeal bulb	8	9	-	-	8			3	8-9	-
Stylet	28	-	-	-	-			1	28	-
Median cirrus	8	9	7	-	7	7,8	1,0	4	7-8	7
Internal cirri	10	11	11	13	12	11,4	1,1	5	10-13	-
External cirri	14	13	15	16	15	14,6	1,1	5	13-16	-
Lateral cirri	14	13	15	16	16	14,8	1,3	5	13-16	16
Primary clavae	5	5	5	5	5	5,0	0,0	5	5	5
Secondary clavae										-
(width x height)	5 x 3	5 x 3	5 x 4	-	5 x 3			4		4 x 2
Cirri E	32	34	-	-	38	34,7	3,1	3	32-38	>22
4th leg sense organ	2	3	2	2	2	2,2	0,4	5	2-3	2

ted separately arising from the lateral head-lobe on a hemispherical platform, clearly delineated from the thicker cuticle of the head plate (Figure 8F). The lateral cirrus (14 µm) is inserted anterior to the primary clava. The primary clava is small and oval (5 µm), with narrowed base. The secondary clava (5 µm x 3 µm) is globular and inserted dorsally, extending slightly beyond the edge of the cephalic plate. All the cephalic cirri consist of a well-developed cirrophore, a long scapus and a short flagellum. Internal cirri (10 µm) and external cirri (14 µm) are inserted ventrally, close to the edge of the frontal part of the cephalic plate. The median cirrus (8 µm) arises mid-dorsally, at the level of the posterior part of the secondary clavae. The cirrus E (32 µm) is inserted dorsally and directly on the caudal plate, without a pedestal (Figure 8E). It consists of an indistinct accordion articulated basal part and a very long and thin tapering flagellum. The sense organ on the fourth leg (2 µm) is a spherical papilla with a small cirrophore and is inserted laterally on the first coxal segment.

The brain is evident inside the head as a large structure refracting the light. It sends out nerves to the different sense organs of the head, where the innervations of the secondary clavae are particularly evident. Two broad extensions of the brain connect to the secondary clavae, and numerous short, hair-like structures (nerve endings?) are visible basally inside the clavae.

The legs seem to be weakly telescopic, with only the tarsus being retractable into the tibia on the first three pairs of legs, whereas the femur is also retractable into the coxa on the fourth pair of legs. There are two claws on each leg. Each claw has a tiny dorsal spur, which is only visible using SEM-technique (Figure 8G, H). All claws originate from short pedestals and are attached to the leg by means of small basal membranes.

The mouth cone is ventral and fully protruded (Figure 7A, B). It is situated close to the anterior margin of the head and consists of a basal part and three telescopic segments. The pharyngeal apparatus (Figure 7B) consists of a buccal tube (26 µm), a pharyngeal bulb (8 µm) and stylets (28 µm). Each stylet is very thin, slightly curved and has a tripartite furca. The pharyngeal bulb is situated in the neck region and has three short placoids. Three horizontal apophyses (internal stylet supports) are inserted between the placoids. Each apophysis has a droplet-shaped terminal swelling. From the pharyngeal bulb, a short oesophagus leads to the diverticulated mid-gut.

The reproductive system of the holotypic female consists of a single ovary bearing one large ovum (21 µm x 26 µm) and two smaller. The ovary is 52 µm long and is attached dorsally beneath the first body plate. The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring (Figure 7D, E and 26). The two cuticular seminal receptacles are formed as small oval pouches situated inside the ventro-lateral triangular processes of the caudal plate. The genital ducts are long, sinuous and open to the exterior, laterally to the gonopore. The anus is terminal and is closed by a three-lobed cuticular system consisting of two large lateral lobes and a small posterior lobe (Figure 7D). A small papilla surmounts the anterior part of the lateral lobes. The posterior part of the anus protrudes from the body (Figures 8D).

The juvenile is 55 µm long from the anterior margin of the head to the base of the caudal plate. Except for the smaller size and the absence of both anus and gonopore, the only notable difference is in the region between the second and third body plate. In the juvenile, there is a considerable distance between the first and second body plate, which could be interpreted as the predisposition of the first intersegmental plate. This plate is apparently lost in the adult.

Remarks: Sharing the morphology of the claws and the secondary clavae, the new genus is superficially similar to the two genera *Pseudostygarctus* and *Mesostygarctus*. However, *Pseudostygarctus* and *Mesostygarctus* possess lateral sheets on the body plates (absent in *Faroestygarctus*) and share a different configuration of the seminal receptacles and gonopore system. The fact that these distinguishing features are considered diagnostic characters of both *Pseudostygarctus* and *Mesostygarctus*, argues against attributing the new species to either of these two genera. Although lateral tapering processes of the body plates without sheets or other extensions are shared by both *Parastygarctus* and *Renaudarctus*, important differences in the morphology of the head plate, primary and secondary clavae and in claw morphology, separate *Faroestygarctus* from both *Parastygarctus* and *Renaudarctus*. In conclusion, the new genus *Faroestygarctus* displays a combination of features which makes it impossible to place it within any of the described genera of Stygarctidae, and the establishment of a new genus is therefore fully justified. It is interesting to note the very small size of the fully mature females of *Faroestygarctus dezioae* that, with a mean body length of 86 µm, makes them the smallest mature females of all known tardigrades. However, two claws per leg is a larval character, thus it is likely that *Faroestygarctus dezioae* exhibits paedomorphosis (Gould 1977). Taking into consideration, not only the claw number and the small body size, but also the very close resemblance between adult and juvenile, *Faroestygarctus dezioae* is probably progenetic rather than neotenic.

Reinstatement of the genus *Mesostygarctus* Renaud-Mornant, 1979

Diagnosis (emended). Stygarctinae with head plate divided into three lobes: posterior part of the head with two lateral lobes bearing the primary clavae; anterior part of the head divided into three lobes by a pair of deep indentations with dorsal cuticular membranes. Three dorsal body plates extending laterally into two similar posterior processes; lateral margin of body plates with cuticular membranes. Two intersegmental dorsal plates. The cuticle is without epicuticular pillars. Large ventral cephalic plate, following the shape of the head. Ventral body plates sometimes present. Longitudinal directed cuticular folds present ventrally on each trunk segment. The primary clavae are elongate club-shaped and the secondary clava are semi-globular. Long tapering cirrus E, telescopically inserted on a lateral process. Each leg with four claws with dorsal spurs. Seminal receptacles formed as large ventral spheroid vesicles or arranged in a spiral internally with looped ducts close to the female gonopore. Seminal receptacle duct openings with internal cuticular bars and external cuticular pockets.

Type species: *Mesostygarctus intermedius* Renaud-Mornant, 1979.

Mesostygarctus spiralis nov. sp. (Figures 9-11 and 27B)

Diagnosis. *Mesostygarctus* with almost semi-circular head plate divided into three lobes: one medial and two lateral lobes. The primary clava is elongate, club-shaped with a spine-like termination; secondary clava semi-globular. Three body plates extending laterally into two similar posterior processes arranged latero-dorsal and latero-ventral; lateral margin of body plates with cuticular membranes. Intersegmental dorsal plate with median sculpture present between first and second body plate and between second and third body plate. The first three trunk segments each bear a large ventral plate. Longitudinal directed cuticular folds present ventrally on each trunk segment. Each leg terminates in four claws with dorsal spurs. Cirrus E telescopically inserted on a large lateral process. Bulb-shaped papilla on the fourth leg. Seminal receptacles arranged in a spiral internally with looped ducts close to the female gonopore.

Material - Holotype female [ZMUC TAR 731] sampled by Niels Svennevig, 28 Aug. 1979 at the rocky shore of Nelson Park (34°10' S; 151°10' E), Sidney, Australia.
Depth range - intertidal.
Sediment type - Carbonate sand originating mostly from eroded serpulidtubes and shell plates from barnacles.
Etymology - The species name "*spiralis*" (Latin) refers to the spiral arrangement of the seminal receptacles.

Holotype: The holotypic female (Figures 9-11 and 27 B) is 146 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle forms seven plates: head plate, three body plates, caudal plate, and two intersegmental plates. The cuticle is without epicuticular pillars and the entire dorsal cuticle is sculptured with numerous, small and perfectly circular depressions (Figure 11A). The head plate is almost semi-circular and with two deep indentations of the lateral margin, dividing the head into three lobes. The indentations are covered by a thin epicuticular membrane (sheet). The dorsal head plate forms a prominent horizontal ridge, extending between the secondary clavae, just slightly anterior to the median cirrus. Mid-dorsally the cuticle forms a longitudinal depression or furrow, extending from the median cirrus towards the first body plate. Between the lateral head lobe and the secondary clava, the thick cuticle of the ventral head plate forms a short acute lateral process adjacent to the secondary clava (Figure 11B).

The three body plates bulge laterally, each having two pairs of similar posterior processes situated ventrally and arranged latero-dorsal and latero-ventral; each process is very short and sharply pointed. A narrow sheet runs along the lateral margin of each body plate. Anteriorly, at the medial plane on the third body plate, the dorsal cuticle forms a small rosette-like sculpture (Figures 10, 11A). The caudal plate has a single pair of lateral processes, on which cirri E are inserted. Mid-dorsally, two circular depressions are present on the caudal plate, probably originating from internal muscle attachments (Figure 11A). The intersegmental dorsal plate between first and second body plate and the one between second and third body plate both have a median oval sculpture with an undulating and heavily jagged margin. A ventral plate is present on each of the first three trunk segments (Figure 11C). The ventral plate of trunk segment 1 is the smallest (18 µm x 12 µm) and appears almost square, whereas the ventral plates of trunk segments 2

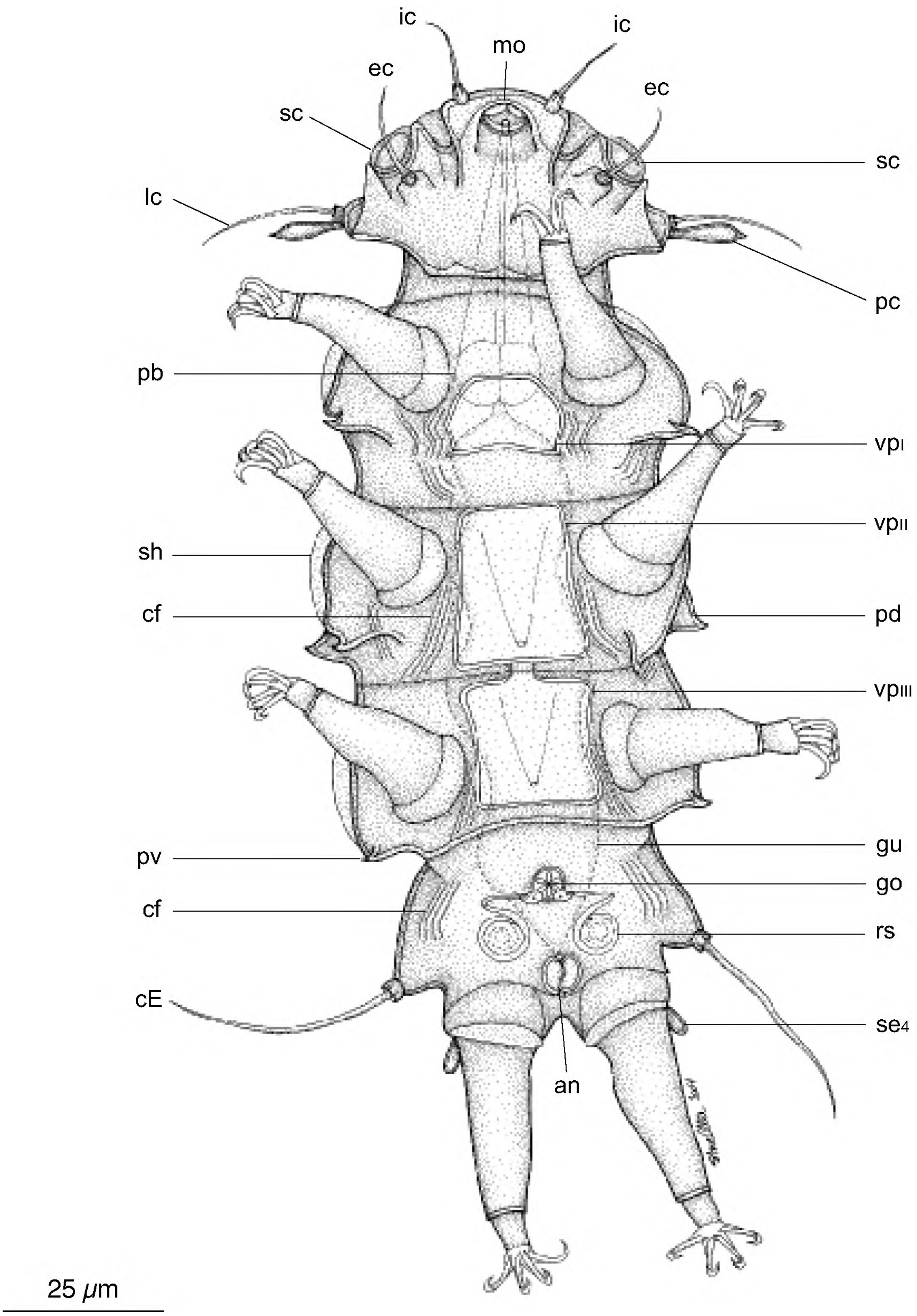


Figure 9. *Mesostygarctus spiralis* nov. sp.: adult holotypic female, ventral view. Drawing by Stine B. Elle.

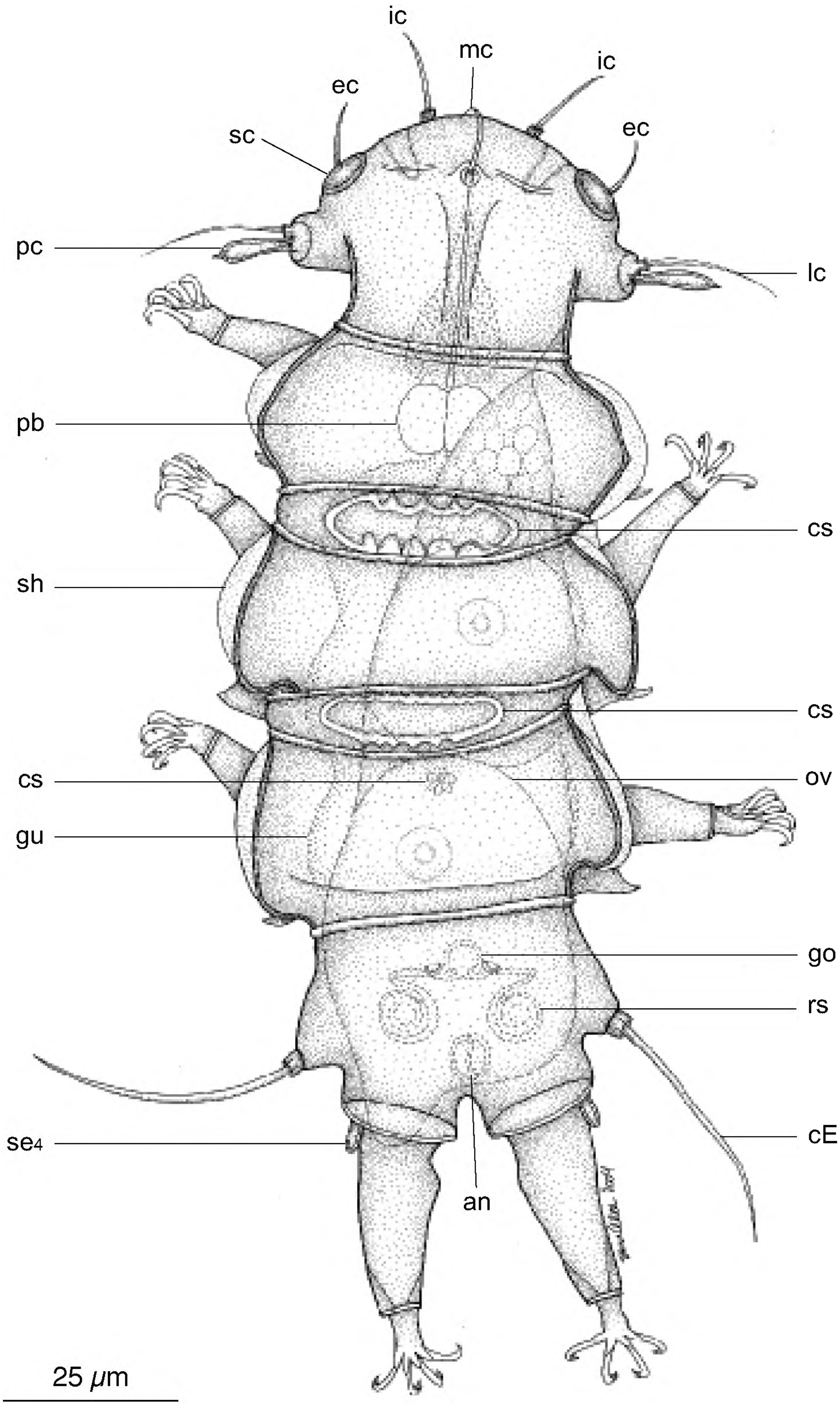
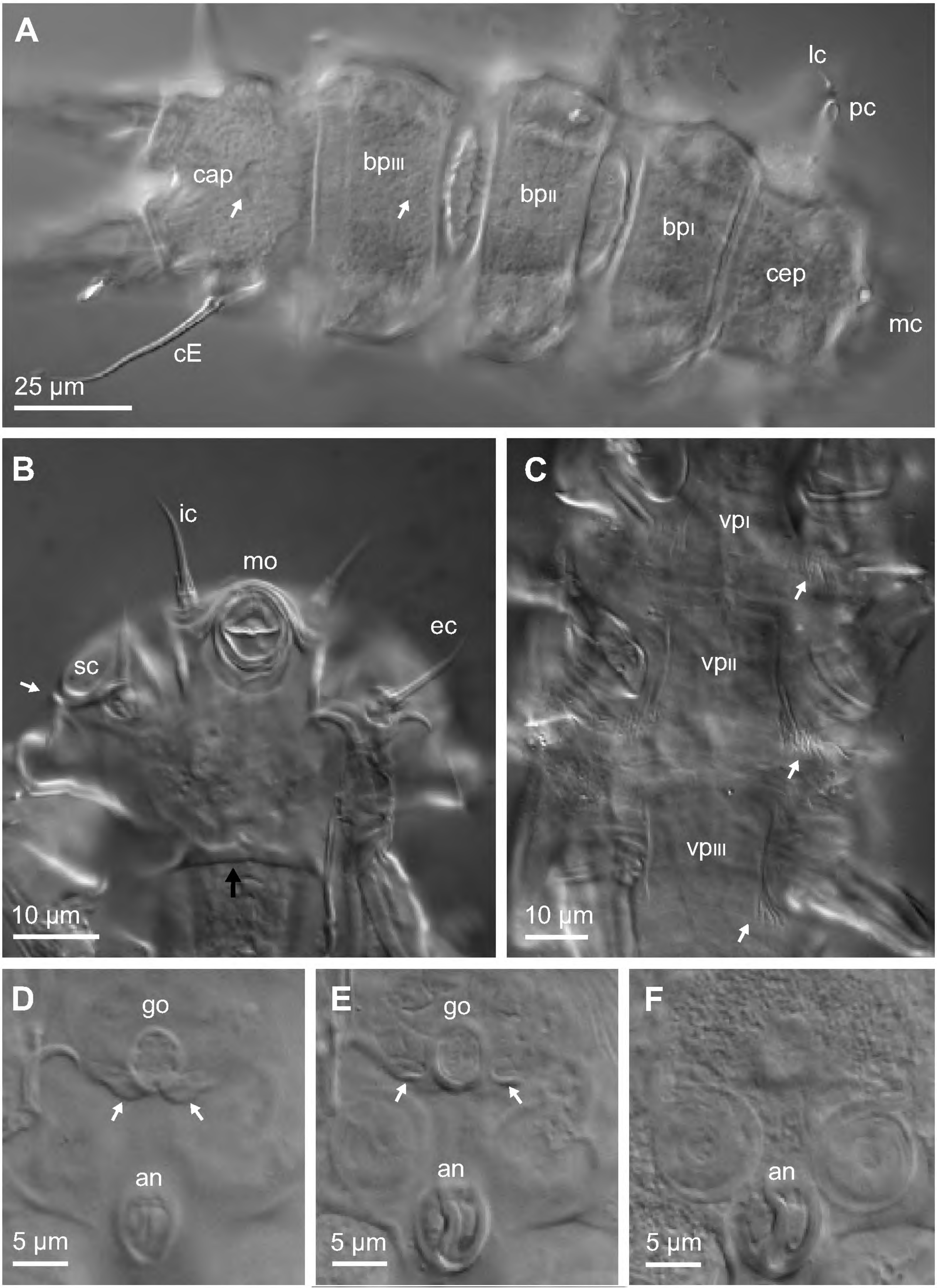


Figure 10. *Mesostygarctus spiralis* nov. sp. : adult holotypic female, dorsal view. Drawing by Stine B. Elle.

Opposite page:

Figure 11. DIC-micrographs of *Mesostygarctus spiralis* nov. sp. A. Dorsal overview, arrows indicate the sculpture of the third body plate and of the caudal plate. B. Detail of the head, ventral view. The white arrow indicates the short acute process adjacent to the secondary clava; the black arrow indicates the edge of the cephalic plate. C. Detail of the ventral plates, arrows indicate the longitudinal cuticular folds. D-F. Optical sections of the gonopore and the seminal receptacles. D. The arrows indicate the external cuticular pockets. E. The arrows indicate the internal cuticular bars. F. Detail of the spiral arrangement of the seminal receptacles.


A
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(18 μm x 25 μm) and 3 (18 μm x 25 μm) are larger and rectangular. The latter two each have an indistinct triangular depression, originating from internal muscle attachments. Para-medial and lateral cuticular folds are present on each trunk segment, appearing like delicate creases of the ventral cuticle (Figure 11C).

A complete set of well-developed cephalic sense organs is present (Figure 11B). Primary clava and lateral cirrus are inserted separately arising from the lateral head-lobe on a hemispherical platform. The lateral cirrus (23 μm) is inserted anterior to the primary clava. The primary clava (14 μm) is elongate, club-shaped with a small terminal spine. The secondary clava (9 μm x 5 μm) is semi-globular and inserted ventrally, extending slightly beyond the edge of the cephalic plate. All the cephalic cirri consist of a well-developed cirrophore, a long scapus and a short flagellum. The internal cirri (15 μm) are inserted on the anterior-frontal edge of the cephalic plate whereas the external cirri (16 μm) are inserted on large ventral pedestals. The median cirrus (13 μm) arises from a small depression of the dorsal cuticle mid-dorsally, slightly posterior to the prominent horizontal ridge of the head plate. The cirrus E (38 μm) is telescopically inserted at the end of a lateral process of the caudal plate. It has a cirrophore with remarkable thick cuticle and a long tapering spine (Figure 11A). The sense organ on the fourth leg (8 μm) is an elongate papilla with rounded termination and is inserted dorso-laterally on the first coxal segmen The legs are highly telescopic, being retractable at all joints. There are four claws on each leg and each internal claw has a tiny dorsal spur. All claws originate from short pedestals and are attached to the leg by means of small basal membranes.

The mouth cone is not fully protruded; however it consists of a basal part and at least two telescopic segments. It is situated ventrally, close to the anterior margin of the head (Figure 11A). The sclerified structures of the pharyngeal apparatus have partly been dissolved, thus only traces of the stylets, the buccal tube (36 μm) and the pharyngeal bulb (13 μm) are still evident. The pharyngeal bulb is situated posterior in the first body segment. From the pharyngeal bulb, a short oesophagus leads to the diverticulated mid-gut.

The reproductive system of the holotypic female consists of a single ovary bearing numerous small oocytes and two very large ova, the posteriormost ovum being the largest (Figure 10). The ovary is 118 μm long and is attached dorsally beneath the cephalic plate. The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring (Figure 11D and 27B). The two cuticular seminal receptacles each form a spiral internally with looped ducts close to the female gonopore (Figure 11F). On each side of the gonopore, an internal cuticular bar is present at the opening of the seminal receptacle duct (Figure 11E). Furthermore, an external cuticular pocket extends from the opening of the seminal receptacle duct and overlaps the gonopore (Figure 11D). The anus is sub-terminal and is closed by a three-lobed cuticular system consisting of two large lateral lobes and a small posterior lobe (Figure 11D-F and 27B). A small papilla surmounts the anterior part of the lateral lobes.

Remarks: *Mesostygarctus spiralis* shares with *M. intermedius* the dorsal plate pattern, the morphology of the head, lateral processes and sheets of the body plates, the morphology of the sense organs and claws and, revealed by the present investigation, the presence of longitudinal ventral cuticular folds. Thus, the new species further consolidates the validity of the genus *Mesostygarctus*, erected by Renaud-Mornant (1979). One of the most important differences between *M. spiralis* and *M. intermedius* is the presence of large ventral plates in *M. spiralis*. Another important difference is the arrangement of the seminal receptacles. The seminal receptacles of *M. intermedius* were not included in the original description of this species. Although our observations on the holotype recognized external genital cuticular pockets, internal structures were not observable. However, the examination of a single specimen of *M. intermedius* from a submarine cave in the Adriatic Sea (see Gallo D'Addabbo et al. 2001), enabled us to describe the seminal receptacles of this species (Figure 27A). The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring. The two cuticular seminal receptacles are formed as large ventral spheroid vesicles with looped ducts close to the female gonopore. Although being weakly defined, an internal cuticular bar is present at the opening of the seminal receptacle duct, on each side of the gonopore. Furthermore, an external cuticular pocket extends from the opening of the seminal receptacle duct and overlaps the gonopore. Instead of having a large spheroid vesicle with a looped duct close to the female gonopore, the duct of the seminal receptacle in *M. spiralis* is wound into a spiral, and terminates in a small vesicle situated in the center of the spiral (Figure 27B).

Genus *Parastygarctus* Renaud-Debyser, 1965

Diagnosis (emended). Stygarctinae with five head lobes, all greatly protruded to about the same extent: one medial, two medio-lateral and two lateral lobes. Body plates extending laterally into one or two gradually tapering long processes. Intersegmental plates between body plates present. Ventral plates sometimes present. Primary and secondary clavae of the same shape, generally elongated. Secondary clavae always situated posterior to the external cirri. Cirrus E with accordion-plated articulation. Each leg with two or four claws, the central pair with a long accessory filament. The vesicle of the seminal receptacle is located dorso-laterally.

Type species: *Parastygarctus higginsi* Renaud-Debyser, 1965.

Parastygarctus robustus nov. sp. (Figures 12, 13 and 29A, Table 5)

Diagnosis. *Parastygarctus* with an almost straight antero-lateral margin of the lateral head lobes. Head plate with a large circular plate bearing the median cirrus. Three body plates, each with a pair of long, acute lateral processes. Caudal plate with a pair of large dorso-lateral processes on which the cirri E are inserted. Both the primary and secondary clavae are elongate, pedunculate club-shaped. Each leg terminates in four claws. Cirrus E comprises four parts; a smooth proximal portion, a bipartite accordion articulated portion followed by a long flagellum. Pedunculate papilla on the fourth leg.

Material - Holotype, female [ZMUC TAR 703] and 4 paratypes, females [ZMUC TAR 704-706, 708] collected 26 April, 1979 by Niels Svennevig at Magdelaine Reef (16°30' S; 150°30' E), North Cay, Australia and 1 paratype, female [ZMUC TAR 707] collected by R.M. Kristensen on the 8 December, 1995 at Wastari reef Heron Island (23°28' S; 151°55' E), Australia.
Depth range Intertidal, within 2 m depth.
Sediment type - Coralline sand.
Etymology - The species name "*robustus*" (Latin) refers to the very robust appearance of this species, especially regarding the large head plate, the processes of the caudal plate and the seminal vesicles.

Holotype: The holotypic female (Figures 12, 13 and 29A) is 142 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle forms seven plates: head plate, three body plates, caudal plate, and two intersegmental plates. The head plate is divided into five greatly protruded lobes: one medial, two medio-lateral and two lateral lobes. Mid-dorsally, at the level of the lateral head lobes, the cuticle forms a large and very characteristic circular plate (Figure 13A). Each of the two lateral head lobes bears a well-developed posterior spine (Figure 13B). The three body plates each have a pair of lateral processes which gradually taper to end in long flexible spines. A prominent, intersegmental dorsal plate is present between first and second body plate and between second and third body plate. Although barely recognisable, each intersegmental plate has median oval sculpture. The caudal plate has a single pair of large, conical dorso-lateral processes, on which cirri E (Figure 13D) are situated. Posteriorly, the caudal plate terminates in two small cuffs, which overlay the coxa of the fourth legs.

A complete set of well-developed cephalic sense organs is present. Primary clava and lateral cirrus are inserted separately arising from the lateral head-lobe. The lateral cirrus (scapus 21 µm, flagellum 15 µm) is inserted anterior to the primary clava. The primary

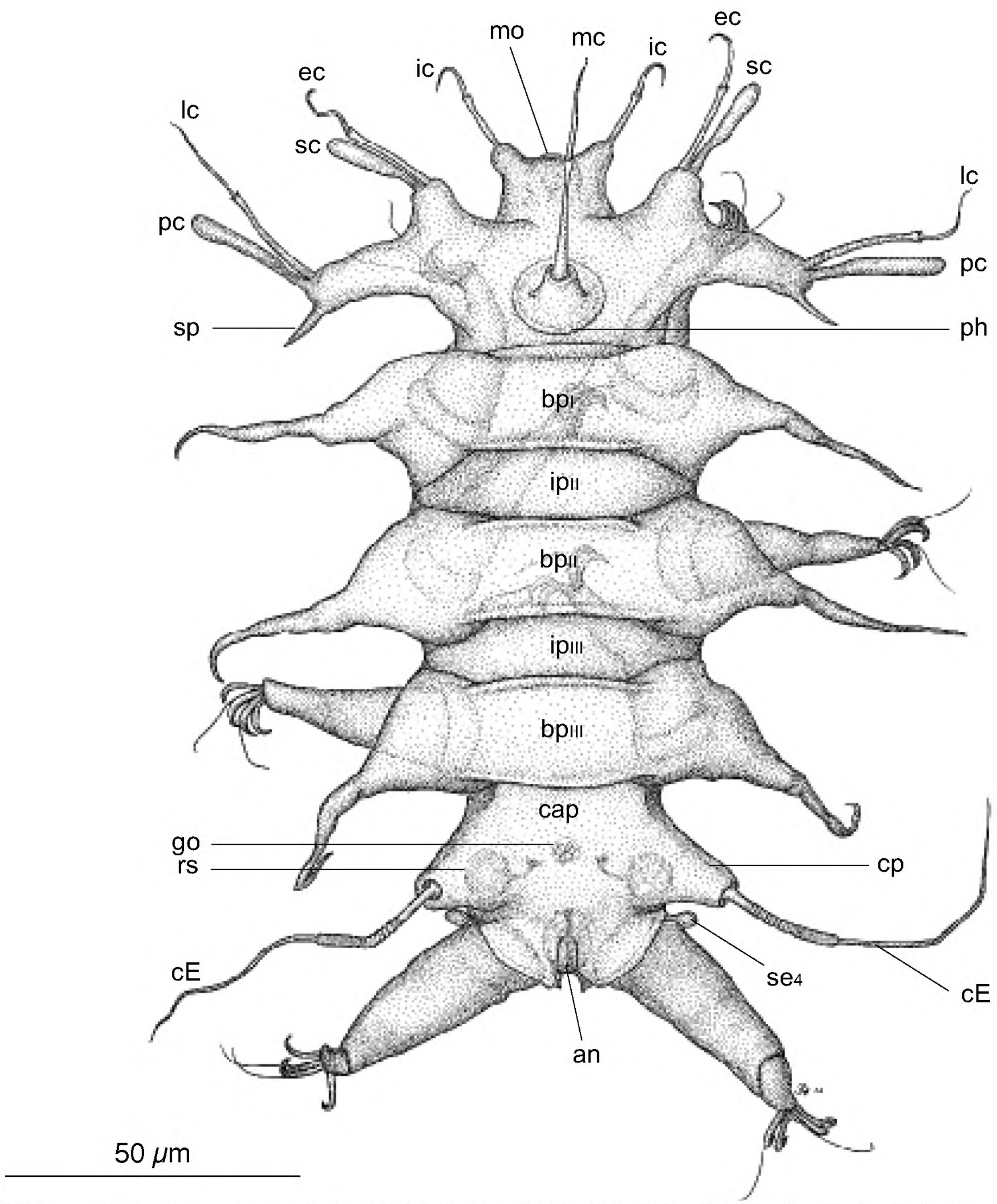


Figure 12. *Parastygarctus robustus* nov. sp.: adult holotypic female, dorsal view. Drawing by Birgitte Rubæk.

clava (24 μm) is a strongly elongate, club-shaped papilla with a well-developed peduncle. The clava is asymmetric, as the transition between the peduncle and the papilla is more apparent on one side of the clava than the other (Figure 13B). The secondary clava (20 μm) arises on the medio-lateral head lobe and is similar in shape, although the asymmetry is even more apparent. Each of the cephalic cirri consists of a long scapus and a slightly shorter flagellum, except the internal cirri where the scapus and the flagellum are of

Figure 13. DIC-micrographs of *Parastygarctus robustus* nov. sp. A. Detail of the head, dorsal view. B. Detail of the primary and secondary clavae; arrows indicate the notch-like constrictions appearing only on one side of the asymmetric clavae. C. Detail of the anus and the female gonopore. D. Detail of the caudal end, dorsal view; note the completely dorsal vesicles of the seminal receptacles.

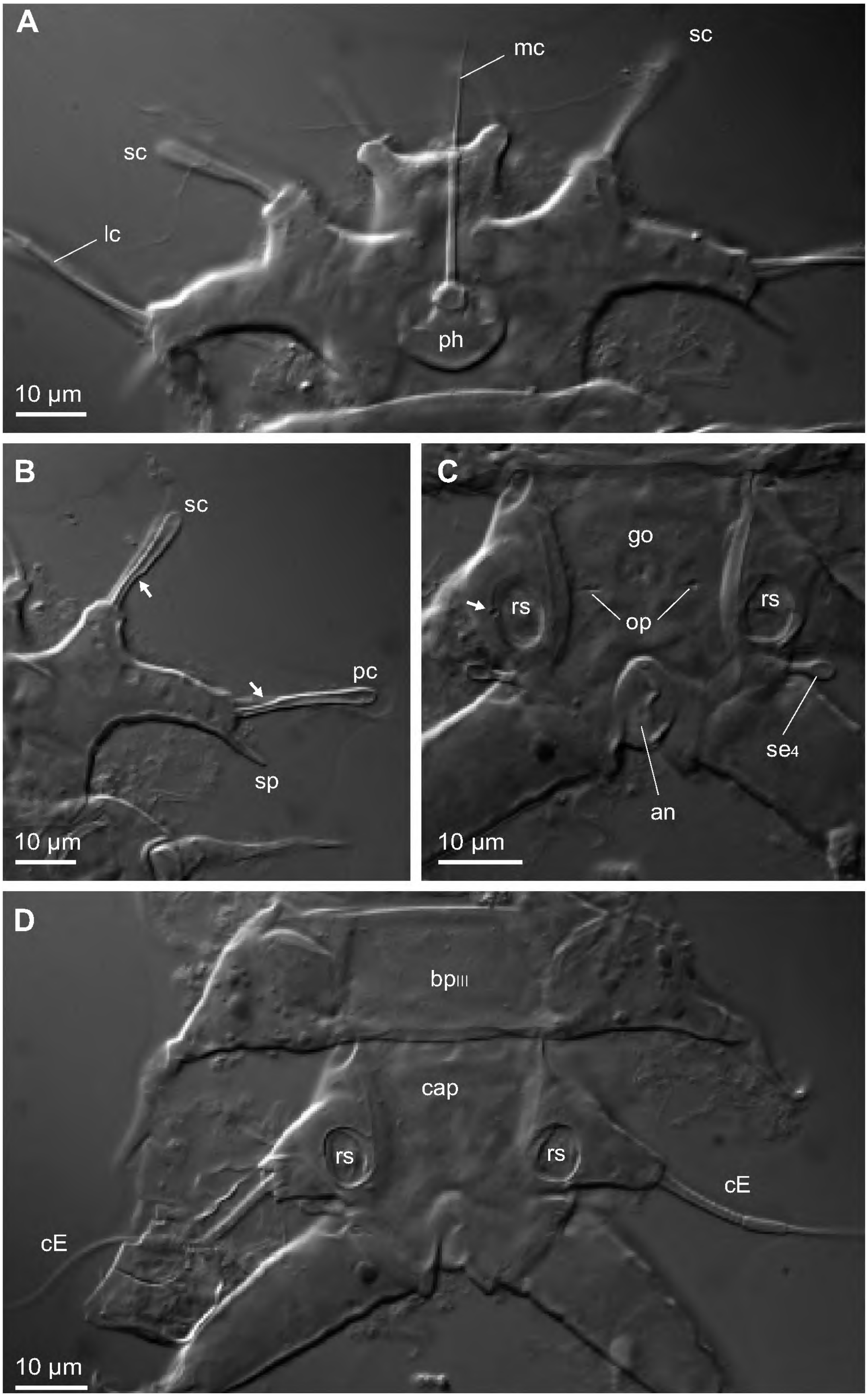


Table 5. Morphometric summary of the specimens of *Parastygarctus robustus* nov. sp. examined and measured in LM. Measurements in µm.

ZMUC no	Holotype female TAR 703	Paratype female TAR 704	Paratype female TAR 705	Paratype female TAR 706	Paratype female TAR 707	Paratype female TAR 708	Mean	St.dev.	n	Range
Body length	142	156	144	165	146	145	149,7	9,0	6	142-165
Median cirrus	34	32	32	37	27	30	32,0	3,4	6	27-37
scapus	20	20	20	20	17	19	19,3	1,2	6	17-20
flagellum	14	12	12	17	10	11	12,7	2,5	6	10-17
Internal cirri	21	17	19	19	17	19	18,7	1,5	6	17-21
scapus	9	9	10	10	9	10	9,5	0,5	6	9-10
flagellum	12	8	9	9	8	9	9,2	1,5	6	8-12
External cirri	29	24	25	27	22	25	25,3	2,4	6	22-29
scapus	16	15	15	16	13	15	15,0	1,1	6	13-16
flagellum	13	9	10	11	9	10	10,3	1,5	6	9-13
Lateral cirri	36	28	29	30	29	30	30,3	2,9	6	28-36
scapus	21	19	19	19	19	20	19,5	0,8	6	19-21
flagellum	15	9	10	11	10	10	10,8	2,1	6	9-15
Primary clavae	24	22	23	24	22	23	23,0	0,9	6	22-24
Secondary clavae	20	18	19	18	16	18	18,2	1,3	6	16-20
Cirri E	45	42	43	44	41	42	42,8	1,5	6	41-45
smooth part	5	4	4	6	4	5	4,7	0,8	6	4-6
loose accordian part	8	9	9	8	6	8	8,0	1,1	6	6-9
annulated part	7	7	6	6	6	6	6,3	0,5	6	6-7
flagellum	25	22	24	24	25	23	23,8	1,2	6	22-25
4th leg sense organ	6	6	6	7	6	7	6,3	0,5	6	6-7

equal length. The internal cirri (scapus 9 µm, flagellum 12 µm) are inserted on the anterior-frontal edge of the medial head lobe whereas the external cirri (scapus 16 µm, flagellum 13 µm) are inserted anterior to the secondary clavae on the two medio-lateral head lobes. The median cirrus (scapus 20 µm, flagellum 14 µm) is the longest of the cephalic cirri and the only one with a well developed cirrophore (Figure 13A). It is inserted on a small pedestal arising from a large circular plate mid-dorsally, at the level of the lateral head lobes. The four-part cirrus E (45 µm) is inserted at the end of a large lateral process (Figure 13D). It has a smooth and relatively short proximal portion (5 µm), a bipartite articulated accordion portion (15 µm) and terminate in a long flagellum (25 µm). The articulated accordion portion consists of a weakly defined proximal section (8 µm), which appears as a stretched accordion, followed by a distal well defined and delicately annulated section (7 µm). The sense organ on the fourth leg (6 µm) consists of a relatively long basal peduncle and a spherical papilla (Figure 13C). It is inserted dorsolaterally on the first coxal segment.

The first three pairs of legs are highly telescopic, being retractable at all joints. The fourth pair of legs is quite different. The cuticle of coxa and tibia is thickened and does not appear to be telescopic, whereas the cuticle of tibia and tarsus are much thinner and highly telescopic. There are four claws on each leg and the medial claws each have a long dorsal filament. All claws are inserted directly on the legs.

The mouth cone is situated sub-terminally and is only partly protruded. Due to the preparation in EPON, the buccal tube, pharyngeal bulb and stylets are no longer recognisable, thus the pharyngeal apparatus cannot be analyzed.

The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring (Figure 13A and 29A). The two cuticular seminal receptacles are formed as large oblong vesicles and situated dorso-laterally, at the level of the dorso-lateral processes of the caudal plate. The genital ducts are long and highly sinuous. They open to the exterior, 6 µm from the gonopore and run ventrally, describing at least three loops before terminating dorsally, into the vesicles. The anus is sub-terminal and is closed by a three-lobed cuticular system consisting of two large lateral lobes and a small anterior papilla.

Remarks: The most conspicuous, and also highly unique, character of *Parastygarctus robustus* nov. sp. is the large circular plate-like sculpture of the head plate, on which the median cirrus is inserted. Another conspicuous character is the shape of the seminal receptacles with highly looped ducts and very large vesicles. Also notable are the large size of the lateral processes of the caudal plate and the terminal cuffs that overlay the coxa of the fourth legs.

Parastygarctus svennevigi nov. sp. (Figures 14-17 and 29B, Table 6)

Diagnosis. *Parastygarctus* with a prominent antero-lateral lobate process on each of the lateral head lobes. Three body plates, each with two pairs of long, acute lateral processes; the anterior is ventral and short, and the posterior is dorsal and long. Caudal plate with two pairs of dorso-lateral processes; the anterior pair on which the cirri E are inserted, and a posterior pair of gradually long tapering processes. Both the primary and secondary clavae are pedunculate elongate club-shaped. Each leg terminates in four claws. Cirrus E is tripartite with a smooth proximal portion, an accordion articulated section and terminating in a long flagellum. Pedunculate papilla on the fourth leg.

Material – Holotype, female [ZMUC TAR 709], allotype, male [ZMUC TAR 710] and 4 paratypes (1 female, 3 males) [ZMUC TAR 711-714] collected 26 April, 1979 by Niels Svennevig at Magdelaine Reef (16°30' S; 150°30' E), North Cay, Australia.
Depth range – Intertidal, within 2 m depth.
Sediment type – Coralline sand.
Etymology – To honour the collector N. Svennevig for his diligent sampling effort, on 12 Australian localities, providing samples containing new species of stygarctids.

Holotype: The holotypic female (Figures 14-17 and 29B, Table 6) is 143 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle forms seven plates: head plate, three body plates, caudal plate, and two intersegmental plates. The head plate is divided into five greatly protruded lobes: one medial, two medio-lateral and two lateral lobes.

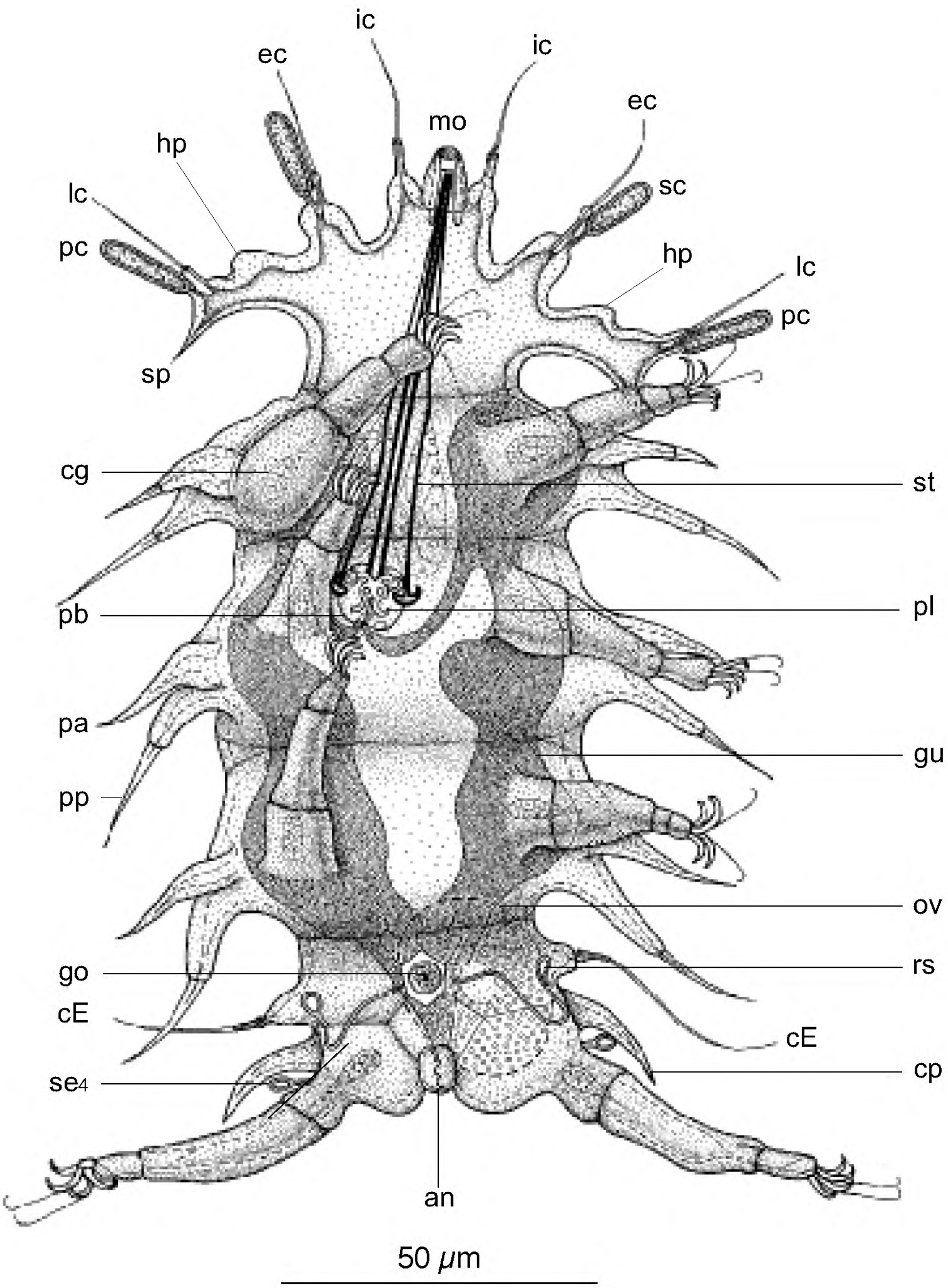
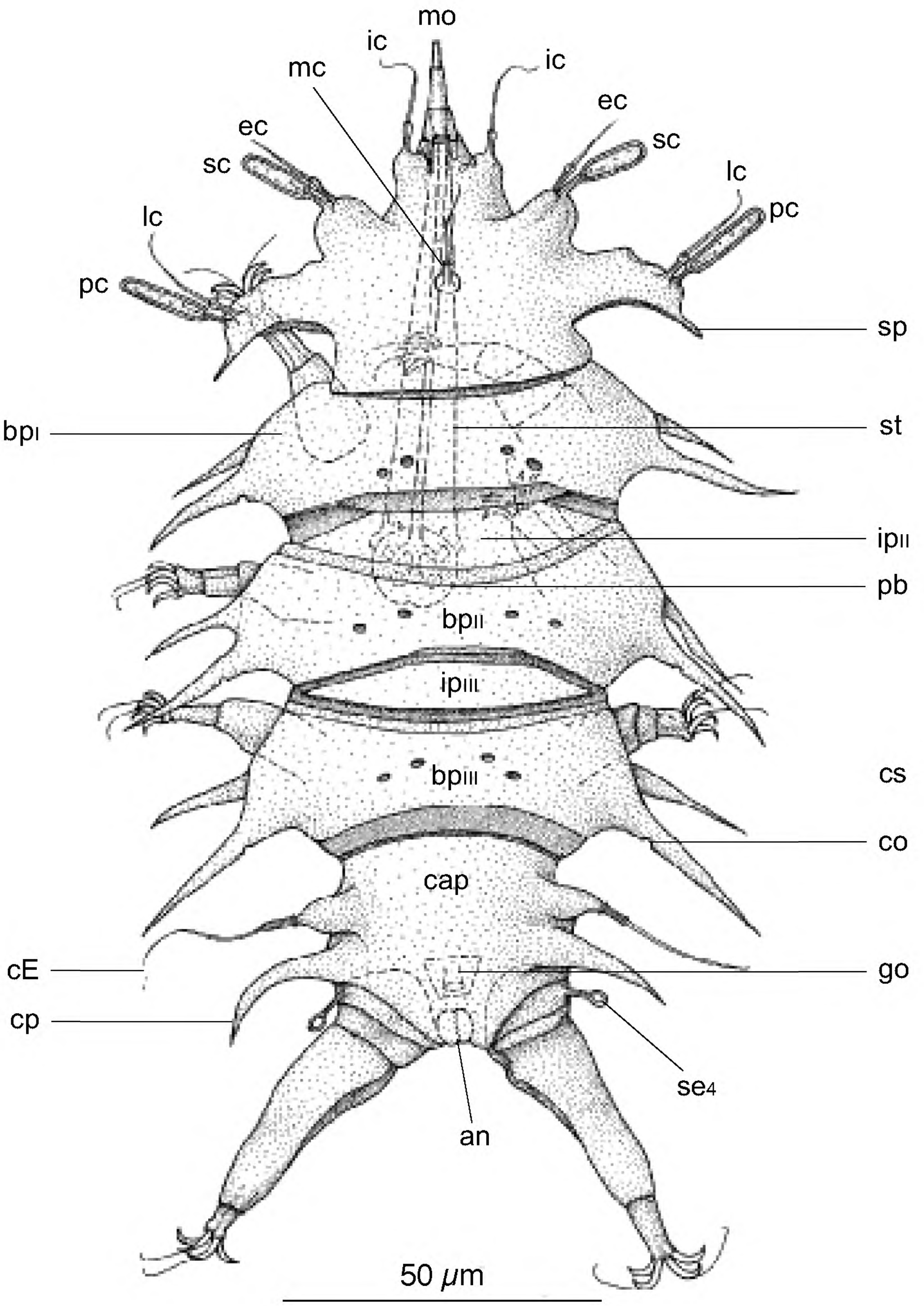


Figure 14. P*arastygarctus svennevigi* nov. sp.: adult holotypic female, ventral view. Drawing by Stine B. Elle.

Each of the two lateral head lobes bears a well-developed posterior spine. A prominent antero-lateral lobate process, also called an elbow (Grimaldi de Zio et al. 1987), is present on each lateral head lobe (Figure 17B). The three body plates each have two pairs of lateral processes. The posterior processes, which are the largest, gradually taper to end in long flexible spines. Each spine has a small notch-like constriction. The anterior processes arise ventrally and are similar to the posterior processes, although considerably smaller. Two bilaterally arranged pairs of small circular depressions are present in the dorsal cuticle of each body plate. Unsculptured intersegmental dorsal plates are present between first and second body plate

Figure 15. *Parastygarctus svennevigi* nov. sp.: adult allotypic male, dorsal view. Drawing by Stine B. Elle.



and between second and third body plate. The caudal plate has two pairs of dorso-lateral processes, of which the anterior pair bears the cirri E. The posterior processes are formed as flexible spines, similar in size and shape to the anterior processes of the body plates.

A complete set of well-developed cephalic sense organs is present. Primary clava and lateral cirrus are inserted separately arising from the lateral head-lobe. The lateral cirrus (scapus 5 μm, flagellum 13 μm) is inserted anterior to the primary clava. The primary clava (18 μm) consists of a short basal peduncle and a terminal elongate, club-shaped papilla with a pronounced transition between the peduncle and the papilla (Figure 17B). The secondary clava (17 μm) arises

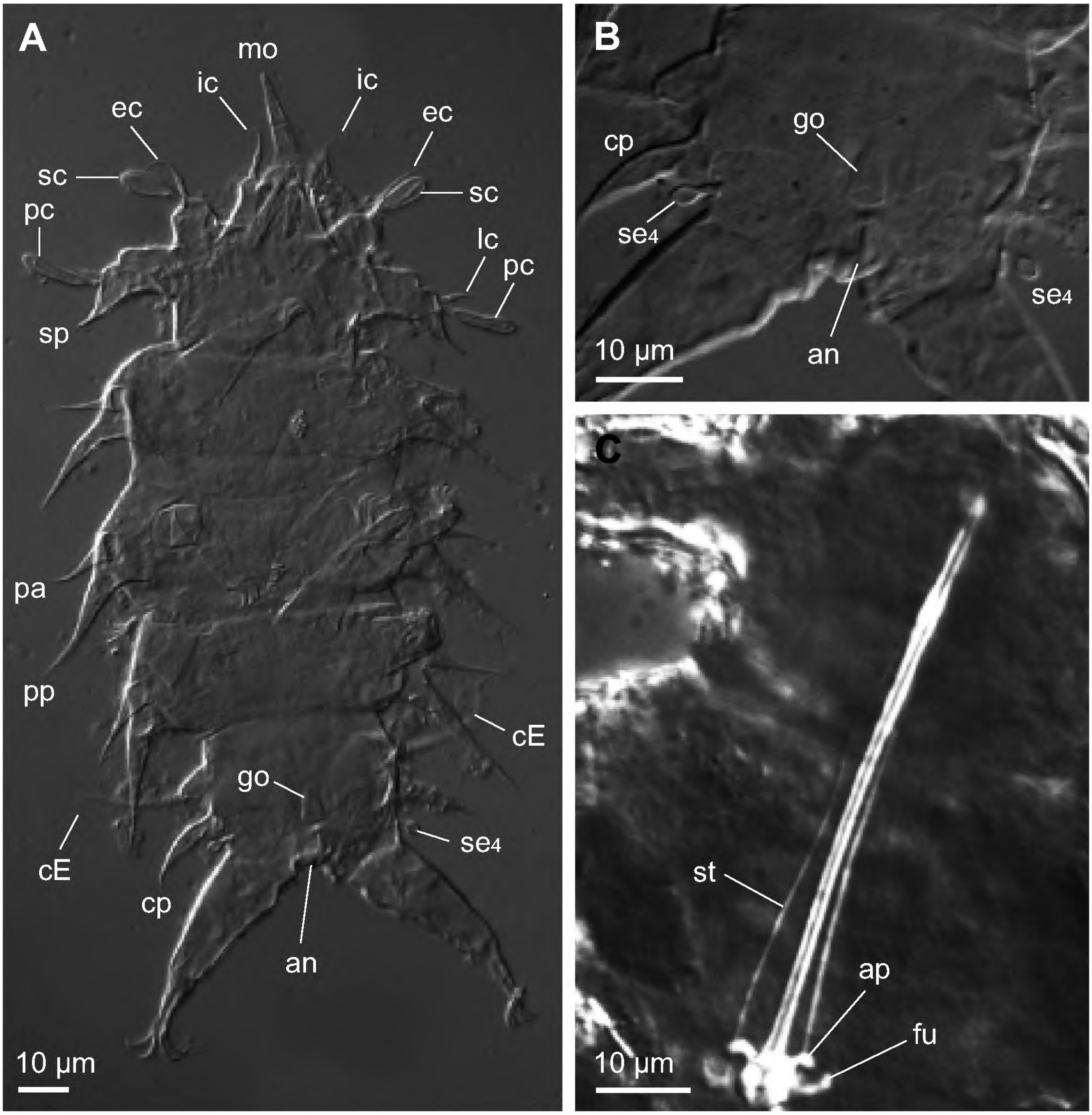


Figure 16. DIC-micrographs of *Parastygarctus svennevigi* nov. sp. A. Ventral overview. B. Detail of the anus and the male gonopore. C. Detail of the bucco-pharyngeal apparatus.

on the medio-lateral head lobe and is similar in shape, although the club-shaped papilla appears less elongated. All the cephalic cirri consist of a short scapus and a long flagellum. The internal cirri (scapus 5 µm, flagellum 17 µm) are inserted on the anterior-frontal edge of the medial head lobe whereas the external cirri (scapus 5 µm, flagellum 17 µm) are inserted anterior to the secondary clavae on the two medio-lateral head lobes. The median cirrus (scapus 3 µm, flagellum 12 µm) arises from a small circular thickening of

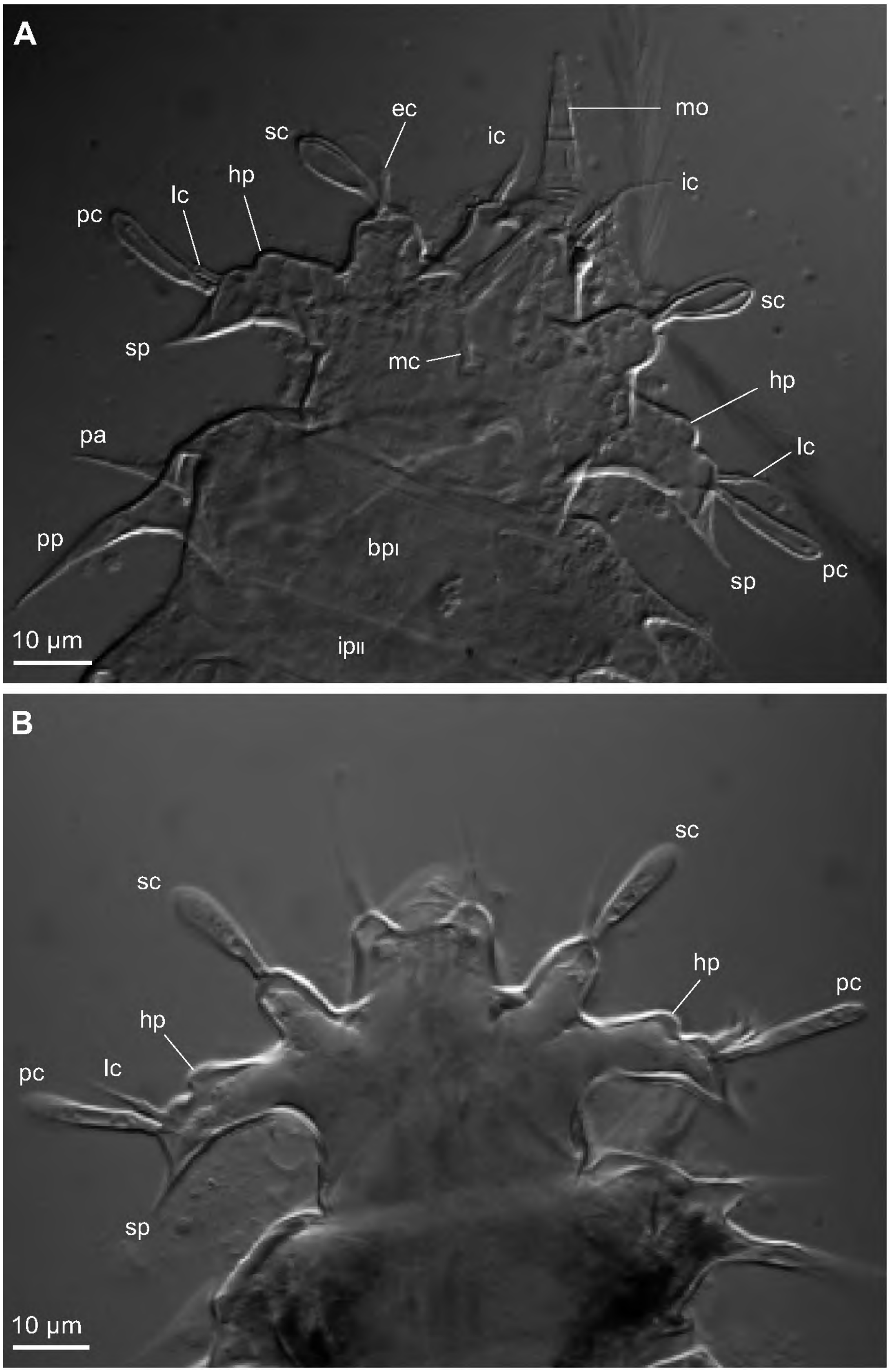


Figure 17. DIC-micrographs of *Parastygarctus svennevigi* nov. sp., lateral contours of the head. A. Male. B. Female.

the dorsal cuticle mid-dorsally, at the level of the lateral head lobes. The tripartite cirrus E (32 µm) is inserted at the end of a large lateral process. It has a smooth and relatively short proximal portion (2 µm), an accordion articulated section (4 µm) and terminating in a long flagellum (26 µm). The sense organ on the fourth leg (7 µm) consists of a relatively long basal peduncle and a spherical papilla. It is inserted dorsolaterally on the first coxal segment.

The legs are highly telescopic, being retractable at

Table 6. Morphometric summary of the specimens of *Parastygarctus svennevigi* nov. sp. examined and measured in LM. Measurements in µm.

	Holotype	**Allotype**	**Paratype**	**Paratype**	**Paratype**	**Paratype**				
	female	**male**	**female**	**male**	**male**	**male**	**Mean**	**St.dev.**	**n**	**Range**
ZMUC no	**TAR 709**	**TAR 710**	**TAR 711**	**TAR 712**	**TAR 713**	**TAR 714**				
Body length	143	135	155	127	142	159	143,5	12,0	6	127-159
Buccal tube	66	55	–	–	–	–	60,5	7,8	2	55-66
Pharyngeal bulb	11	12	–	–	–	–	11,5	0,7	2	11-12
Stylet	70	62	–	–	–	–	66,0	5,7	2	62-70
Median cirrus	–	15	14	12	12	15	13,6	1,5	5	12-15
scapus	–	3	4	4	4	4	3,8	0,4	5	3-4
flagellum	–	12	10	8	8	11	9,8	1,8	5	8-12
Internal cirri	22	19	19	18	16	17	18,5	2,1	6	16-22
scapus	5	4	5	4	4	5	4,5	0,5	6	4-5
flagellum	17	15	14	14	12	12	14,0	1,9	6	12-17
External cirri	22	14	17	16	17	18	17,3	2,7	6	16-22
scapus	5	5	4	5	4	5	4,7	0,5	6	4-5
flagellum	17	9	13	11	13	13	12,7	2,7	6	9-17
Lateral cirri	18	18	19	18	16	21	18,3	1,6	6	16-21
scapus	5	6	5	5	4	5	5,0	0,6	6	4-6
flagellum	13	12	14	13	12	13	12,8	0,8	6	12-14
Primary clavae	18	18	20	17	18	21	18,7	1,5	6	17-20
Secondary clavae	17	16	16	15	15	17	16,0	0,9	6	15-17
Cirri E	32	29	32	30	26	30	29,8	2,2	6	26-32
smooth part	2	2	3	2	2	2	2,2	0,4	6	2-3
annulated part	4	4	5	5	4	5	4,5	0,5	6	4-5
flagellum	26	23	24	23	20	23	23,2	1,9	6	20-26
4th leg sense organ	7	7	8	6	7	9	7,3	1,0	6	6-9

all joints. There are four claws on each leg and the medial claws each have a long dorsal filament (Figures 14 and 15). All claws are inserted directly on the legs.

The mouth cone is situated in anterior terminal position and consists of a basal section and three telescopic segments. The pharyngeal apparatus consists of buccal tube (66 µm), pharyngeal bulb (11 µm) and stylets (70 µm). Stylet supports are missing. Each stylet is long and thin and has a bifurcate stylet furcae that bend anteriorly. The stylets are slightly sinuous in a way that indicates some flexibility (Figure 16C). (Normally the stylets are rigid, nonflexible structures in *Parastygarctus* species). The pharyngeal bulb is situated anteriorly in the second body segment and has three short placoids. Each placoid bends outwards and has an anterior globular swelling. Three upright apophyses bend posteriorly (internal stylet supports) are inserted between the placoids anteriorly. Each apophysis has a small droplet-shaped terminal swelling (Figure 16C). From the pharyngeal bulb, a short oesophagus leads to the highly diverticulated mid-gut which has a strong green colour.

The reproductive system of the holotypic female consists of a single ovary bearing a single large ovum. The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring (Figure 29B). The two cuticular seminal receptacles are formed as small oval vesicles situated inside the anterior pair of dorso-lateral processes of the caudal plate. The genital ducts are long, sinuous and open to the exterior, close to the gonopore. The anus is sub-terminal and is closed by a three-lobed cuticular system consisting of two large lateral lobes and a small posterior lobe.

Allotype: The allotypic male (Figures 15, 16 and 17A, Table 6) is 135 µm long from the anterior margin of the head to the base of the caudal plate. No strong sexual dimorphism is observed in *Parastygarctus svennevigi* nov. sp. In the male, the two medio-lateral head lobes are broader than in the female and the secondary clavae are more ovoid (Figure 17A). The male gonopore is formed as a broad tube with a large oval opening (Figure 16B).

Remarks: The most prominent feature distinguishing *Parastygarctus svennevigi* nov. sp. from other congeneric members, is the arrangement and shape of the lateral processes of the caudal plate. In *P. svennevigi* nov. sp. the caudal plate has two pairs of dorso-lateral processes, of which the anterior processes bears cirri E and the posterior processes are gradually tapering spines. *P. biungulatus* is the only other species possessing gradually tapering caudal processes, however, in this species cirri E are not inserted on caudal processes. Other prominent characters includes a long peduncle of the forth leg sense organ only shared by *P. renaudae* and *P. robustus* nov. sp., and a short scapus of all cephalic cirri only shared by *P. mediterranicus*.

Genus *Pseudostygarctus* McKirdy, Schmidt & McGinty-Bayly, 1976

Diagnosis (emended). Stygarctinae with head plate usually divided into five lobes: posterior part of the head with two lateral lobes bearing the primary clavae; anterior part of the head usually divided into five lobes by two pairs of deep indentations with cuticular membranes. Three body plates each extending laterally into two processes; lateral margin of body plates with thin cuticular membranes. Two intersegmental dorsal plates; ventral plates sometimes present. The primary clavae are elongate club-shaped and the secondary clava are semi-globular. Cirrus E with "ball and socket" articulation. Each leg with four, three or two claws; claws simple or with dorsal spurs. Seminal receptacles formed as large ventral spheroid vesicles with looped ducts close to the female gonopore. Seminal receptacle duct openings with internal cuticular bars and external cuticular pockets.

Type species: *Pseudostygarctus triungulatus* McKirdy, Schmidt & McGinty-Bayly, 1976.

Pseudostygarctus galloae nov. sp. (Figures 18-21 and 27C, Table 7)

Diagnosis. *Pseudostygarctus* with almost semi-circular head plate divided into five lobes: one medial, two

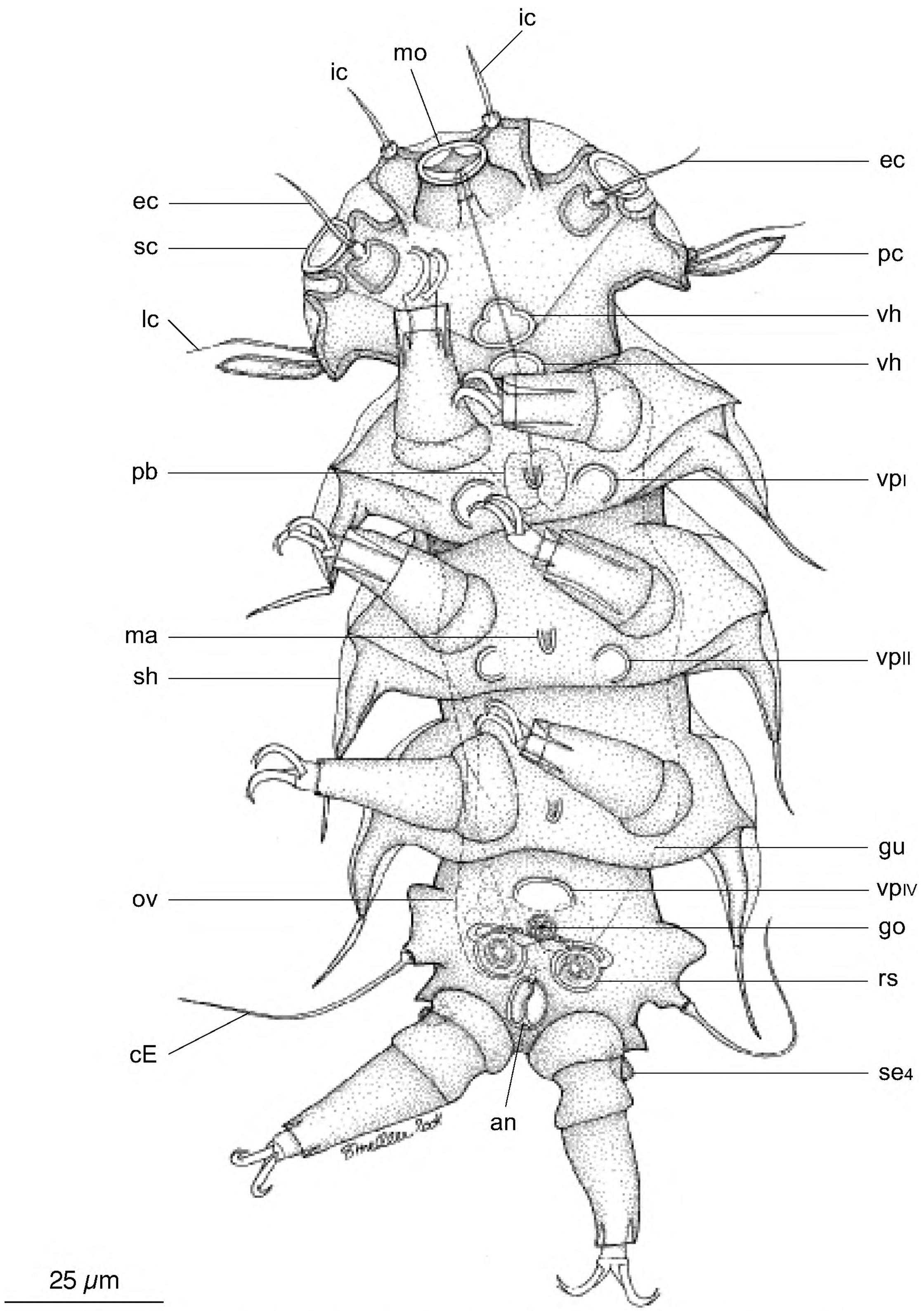


Figure 18. *Pseudostygarctus galloae* nov. sp.: adult holotypic female, ventral view. Drawing by Stine B. Elle.

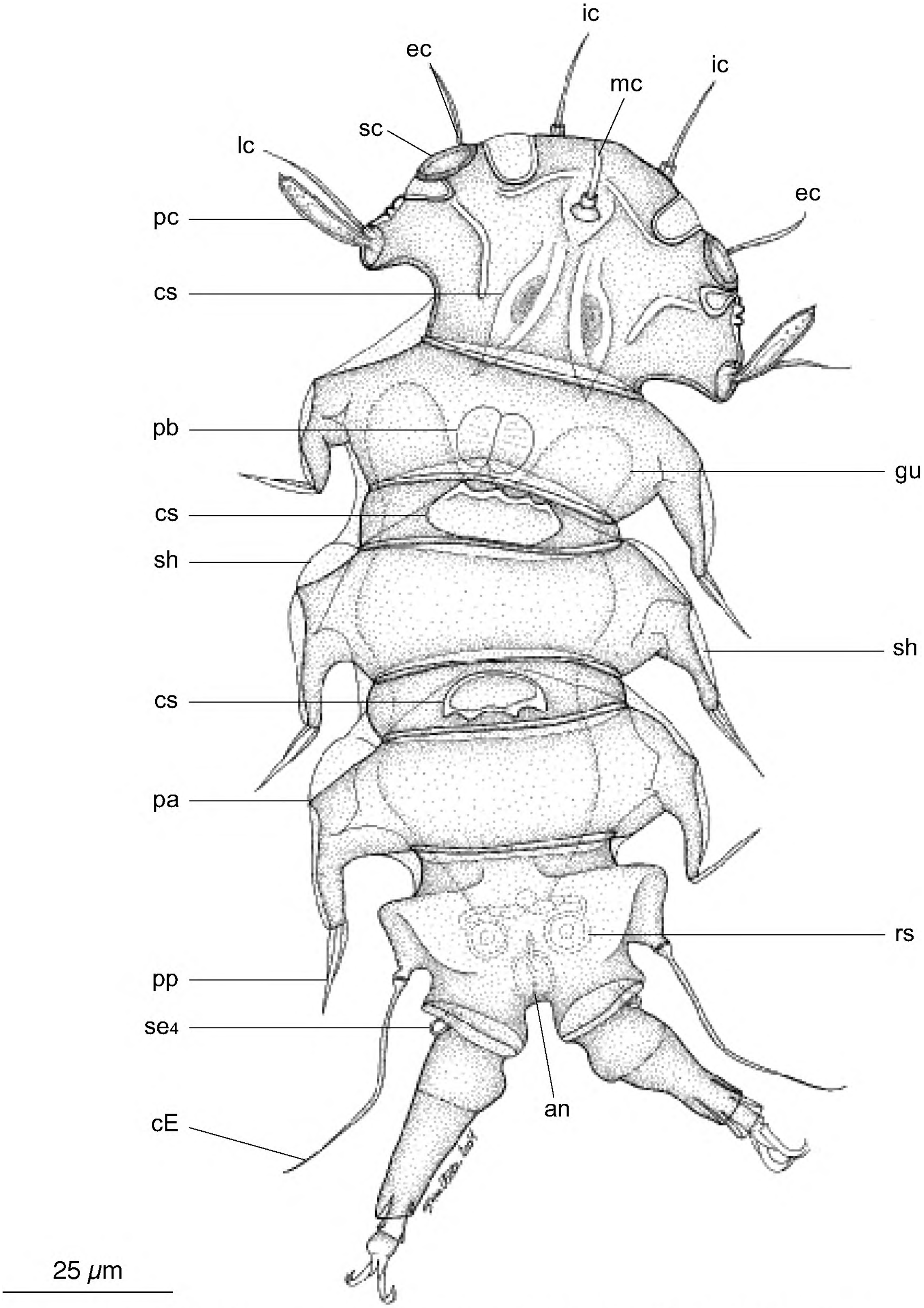


Figure 19. *Pseudostygarctus galloae* nov. sp.: adult paratypic female, dorsal view. Drawing by Stine B. Elle.

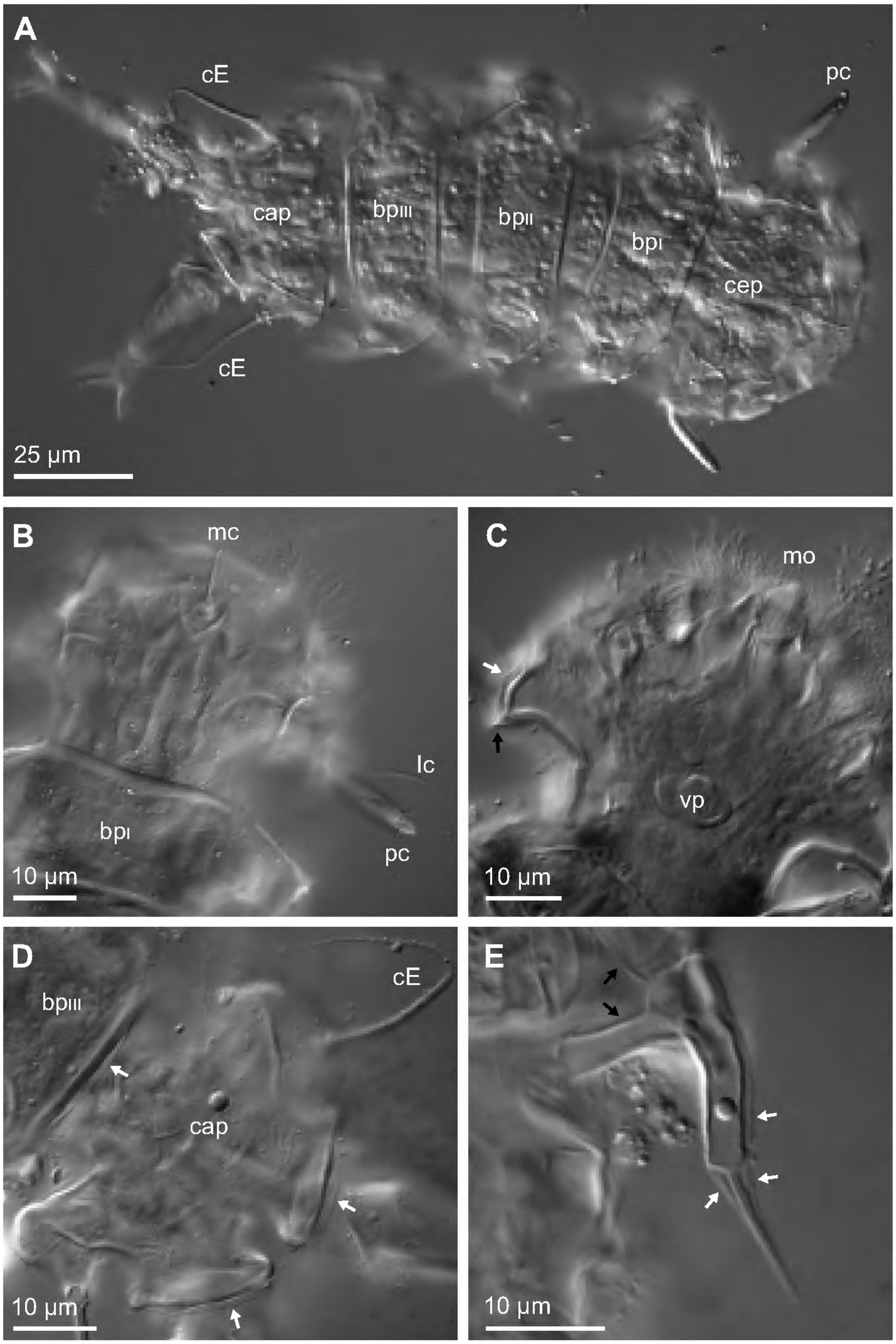


Figure 20. DIC-micrographs of *Pseudostygarctus galloae* nov. sp. A. Dorsal overview. B. Detail of the head and the dorsal cuticular sculpture. C. Detail of the head, ventral view, and the small ventral plate; the black arrow indicates the short acute process of the lateral head lobe; the white arrow indicates the narrow sheet of the lateral head lobe. D. Detail of the caudal plate, dorsal view; arrows indicate the small cuticular sheets of the plates. E. Detail of the lateral process of the third body plate; the white arrows indicate the narrow sheets of the lateral process; the black arrows indicate the heavily cuticularized branching ridges.

medio-lateral and two lateral lobes. The primary clava is elongate, club-shaped; secondary clava semi-globular. Three body plates, each with two pairs of lateral processes, the anterior processes are very short and sharply pointed; margin of body plates with narrow cuticular sheet. Ventral surface of lateral processes with heavily cuticularized branching ridges. Intersegmental dorsal plate with median sculpture present between first and second body plate and between second and third body plate. Caudal plate with a pair of late-

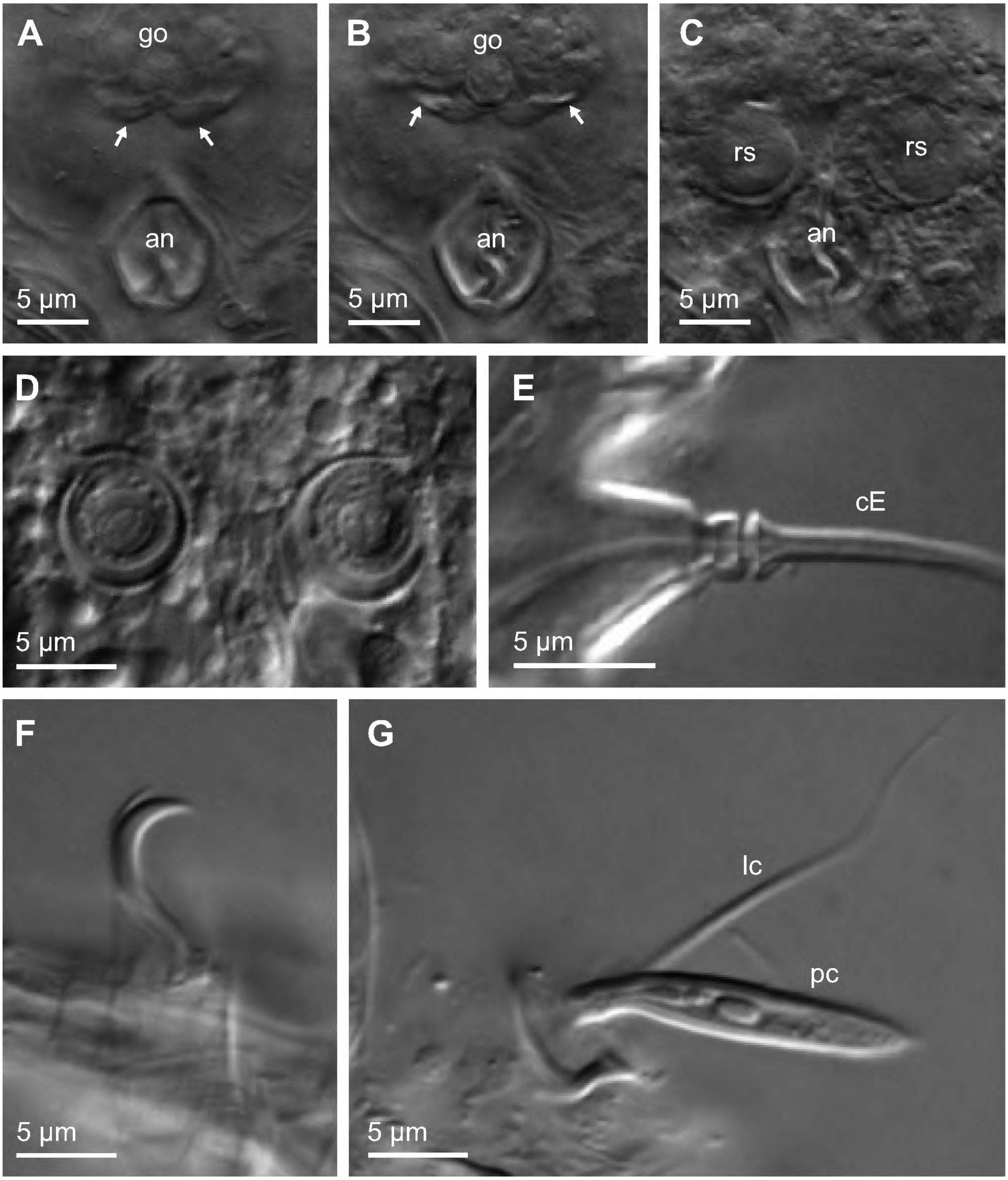


Figure 21. DIC-micrographs of *Pseudostygarctus galloae* nov. sp. A-D. Optical sections of the gonopore and the seminal receptacles. A. The arrows indicate the external cuticular pockets. B. The arrows indicate the internal cuticular bars. C. Detail of the perfectly spherical vesicles of the seminal receptacles. D. Close-up on vesicles with spermatids. E. Detail of the "ball and socket" articulation of the cirrus E. F. Detail of the claw of leg four. G. Detail of the internal structure of the primary clava.

Table 7. Morphometric summary of the specimens of *Pseudostygarctus galloae* nov. sp. examined and measured in LM. Measurements in µm.

ZMUC no	**Holotype female TAR 725**	**Paratype female TAR 726**	**Paratype female TAR 727**	**Paratype female TAR 728**	**Paratype female TAR 729**	**Mean**	**St.dev.**	**n**	**Range**	**Paratype juvenile TAR 730**
Body length	150	132	135	146	157	144,0	10,4	5	132-157	124
Buccal tube	47	–	–	40	–	43,5	4,9	2	40-47	36
Pharyngeal bulb	10	13	–	12	–	11,7	1,5	3	10-13	11
Stylet	–	–	–	–	–	–	–			–
Median cirrus	10	7	10	11	9	9,4	1,5	5	7-11	7
Internal cirri	14	17	14	11	15	14,2	2,2	5	11-17	14
External cirri	19	16	16	19	19	17,8	1,6	5	16-19	15
Lateral cirri	20	20	19	26	20	21,0	2,8	5	19-26	16
Primary clavae	18	17	17	17	16	17,0	0,7	5	16-18	14
Secondary clavae (width x height)	10 x 5	9 x 5	9 x 5	10 x 5	10 x 4			5		– 8 x 4
Cirri E	38	36	36	38	33	36,2	2,0	5	33-38	33
4th leg sense organ	6	5	6	7	6	6,0	0,7	5	5-7	4

ral triangular processes. The cephalic segment and the first two body segments each bear a pair of small ventral plates; the caudal segment bears a single ventral plate. Each leg terminates in two claws with dorsal spurs. Cirrus E inserted on a large lateral process.

Material – Holotype, female [ZMUC TAR 725] and 5 paratypes (4 females, 1 juvenile) [ZMUC TAR 726-730] collected by the ARAMCO project 30 July, 1982 at Ras Al Tanajib (27°47' N; 48°53' E), Arabian Gulf, Saudi Arab
Depth range – Intertidal.
Sediment type – A mixture of carbonate sand and quartz grains.
Etymology – To honour Prof. Maria Gallo D'Addabbo, in particular for her work on the genus *Pseudostygarctus*.

Holotype: The holotypic female (Figures 18, 20C, E, 21D, E and 27C) is 150 µm long from the anterior margin of the head to the base of the caudal plate. The dorsal cuticle forms seven plates: head plate, three body plates, caudal plate, and two intersegmental plates (Figure 20A). The head plate is almost semicircular and with four deep indentations of the lateral margin, dividing the head into five lobes. The indentations are covered by a thin cuticular membrane. Dorsally, the head plate appears quite rugged, with numerous depressions and ridges (Figure 20B). Three curved cuticular ridges are particularly evident; one horizontal ridge, anterior to the median cirrus, and two transverse ridges at the postero-lateral indentations of the head. Mid-dorsally the cuticle forms two very characteristic lanceolate sculptures. A narrow sheet is evident along the frontal margin of the medial head lobe, between the internal cirri. The dorsal contour of the part of the lateral head lobe between the postero-lateral indentation and the primary clava is different from the ventral contour. Dorsally, the thick cuticle of the head plate forms small blunt teeth, thus the dorsal margin appears serrated (Figure 20B).

Ventrally, the thick cuticle forms a short acute lateral process at the posterior rim of the lateral head lobe (Figure 20C - black arrow). A narrow sheet runs along the ventral margin of the lateral head lobe, between the postero-lateral indentation and the short lateral process (Figure 20C - white arrow). The three body plates each have two pairs of lateral processes. The anterior processes are very short and sharply pointed, each with a small, but well-developed semi-circular sheet. The posterior processes gradually taper and end in flexible spines. A narrow sheet runs along the lateral margin of each process, extending from the tip of the anterior process to the base of the flexible spine. On both sides of the spine, a narrow sheet narrows from the base towards the tip of the spine (Figure 20E - white arrow). Narrow sheets are also evident along both the anterior and the posterior margins of each body plate and caudal plate (Figure 20D). The ventral surface of the lateral processes has the same heavily cuticularized branching ridges (Figure 20E - black arrow) as observed in *Pseudostygarctus triungulatus*. The caudal plate has two pairs of lateral triangular processes, of which the posterior pair bears cirri E. The intersegmental dorsal plate between first and second body plate has a median oval sculpture with an undulating anterior margin. The intersegmental dorsal plate between second and third body plate has a similar sculpture, with an undulating posterior margin. Two small mid-ventral plates are present in the neck region of the cephalic segment: a three-lobed anterior plate and a semi-circular posterior plate. A pair of small ventral semi-circular plates are present posterior to the leg pair of trunk segments 1 and 2, and a single ventral plate is present on the caudal segment, situated slightly anterior to the gonopore.

A complete set of well-developed cephalic sense organs is present. Primary clava and lateral cirrus are inserted separately arising from the lateral head-lobe on a hemispherical platform. The lateral cirrus (20 µm) is inserted anterior to the primary clava. The primary clava (18 µm) is elongate, club-shaped with a small terminal spine (Figure 21G). The secondary clava (5 µm x 10 µm) is semi-globular and inserted ventrally, extending slightly beyond the edge of the cephalic plate. All the cephalic cirri consist of a well-developed cirrophore, a long scapus and a short flagellum. The internal cirri (14 µm) are inserted on the antero-frontal edge of the cephalic plate whereas the external cirri (19 µm) are inserted on large ventral pedestals. The median cirrus (10 µm) arises from a small depression of the dorsal cuticle mid-dorsally, at the level of the posterior part of the secondary clavae. The cirrus E (38 µm) is inserted at the end of a large lateral process and has a "ball and socket" articulation (Figure 21E). The sense organ on the fourth leg (6 µm) is a pedunculate papilla with rounded termination and is inserted dorso-laterally on the first coxal segment.

The legs are highly telescopic, being retractable at all joints. There are two claws on each leg and each claw has a tiny dorsal spur (Figure 21F). All claws originate from short pedestals and are attached to the leg by means of small basal membranes.

The mouth cone consists of a basal part and three telescopic segments. It is situated ventrally, close to the anterior margin of the head. The sclerified structures of the pharyngeal apparatus has been dissolved by the mounting media in the studied specimens, thus only the buccal tube (47 µm) and the pharyngeal bulb (10 µm) are still evident. The pharyngeal bulb is situated posteriorly in the first body segment. From the pharyngeal bulb, a short oesophagus leads to the diverticulated mid-gut.

The reproductive system of the holotypic female consists of a single ovary bearing numerous small oocytes. The ovary is 30 µm long and is attached dorsally beneath the second body plate. The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring (Figures 21A-B and 27C). The two cuticular seminal receptacles are formed as large ventral spheroid vesicles with looped ducts close to the female gonopore (Figure 21C). On each side of

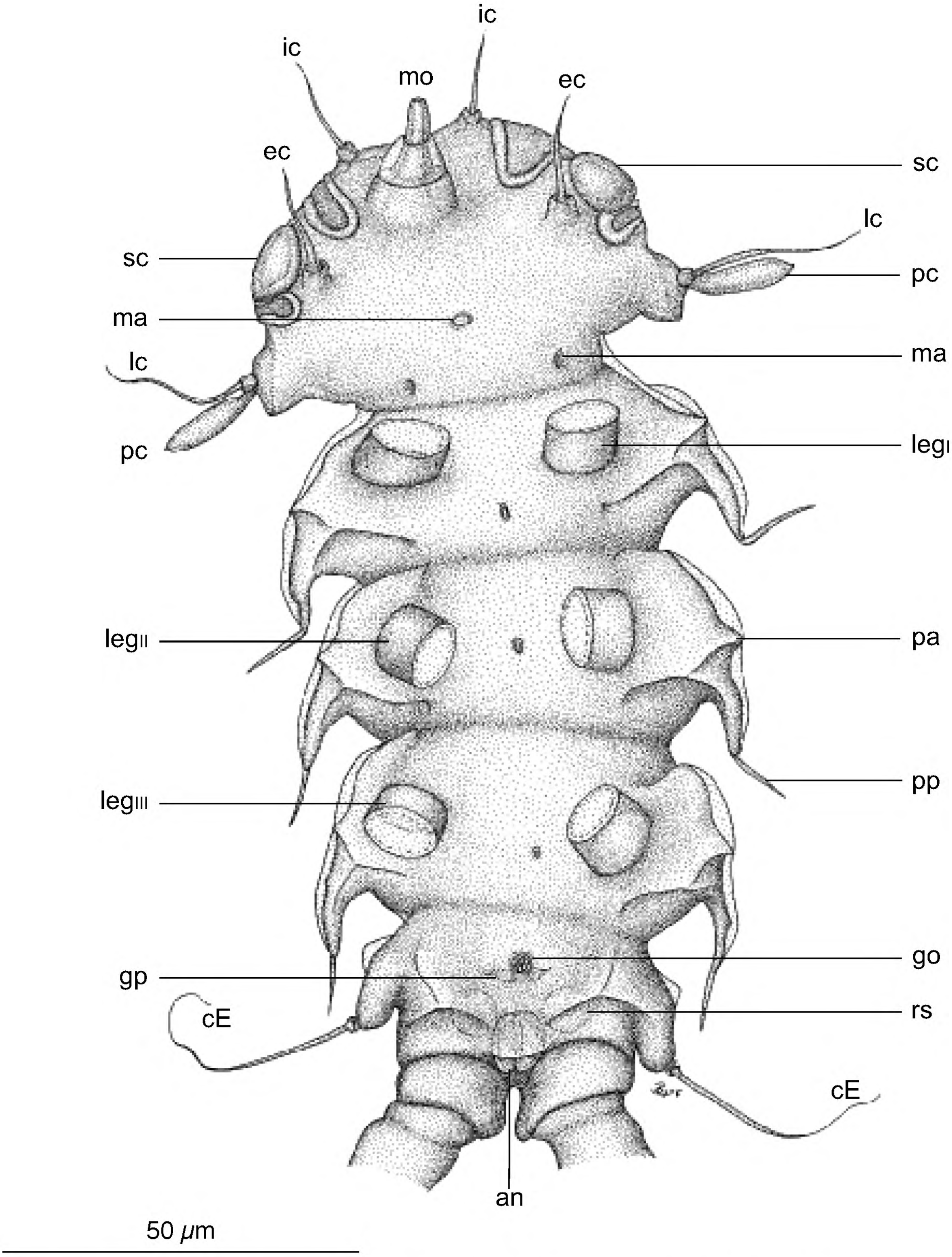


Figure 22. *Pseudostygarctus triungulatus*: adult holotypic female, ventral view. Drawing by Birgitte Rubæk.

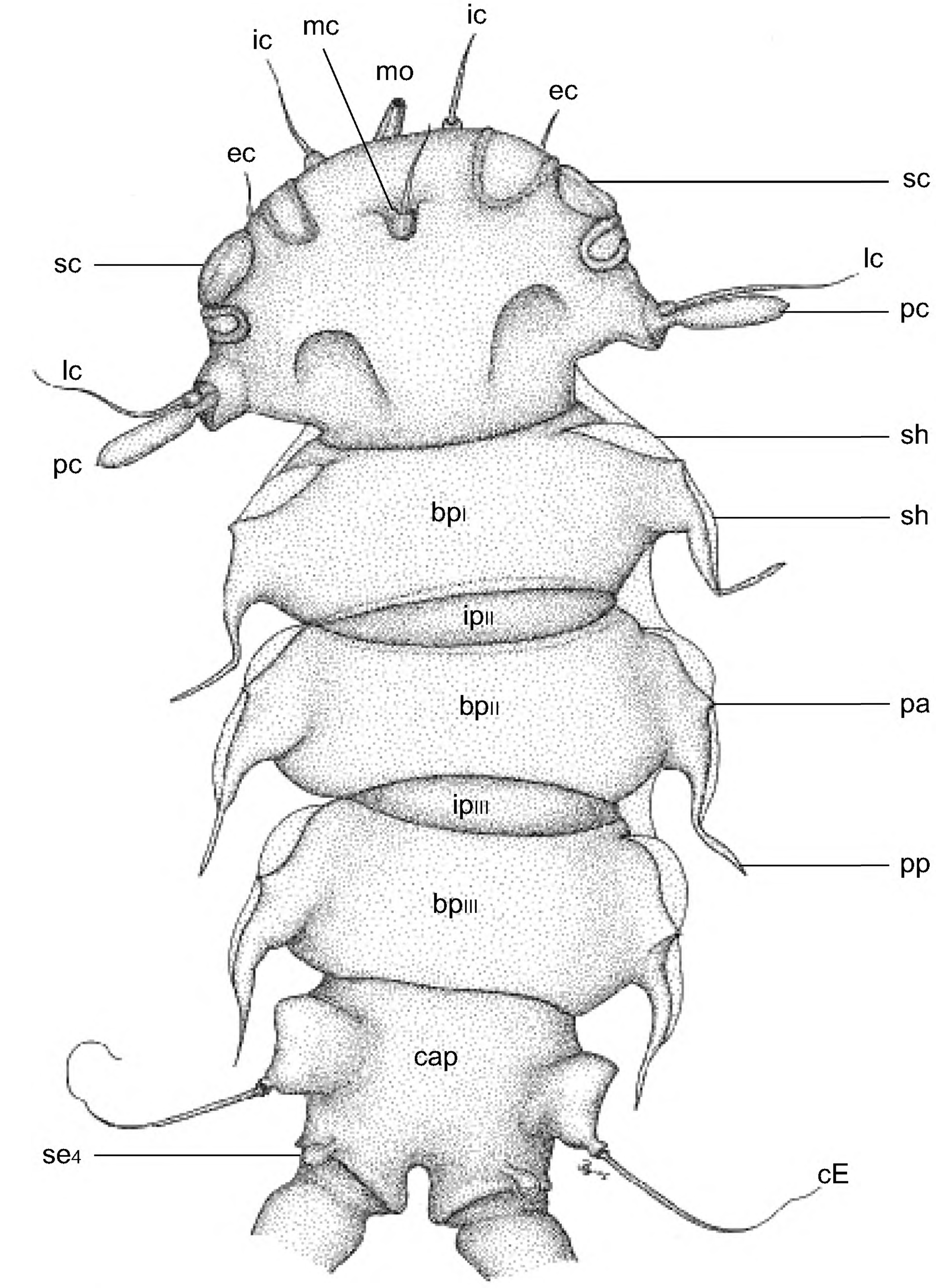


Figure 23. *Pseudostygarctus triungulatus*: adult holotypic female, dorsal view. Drawing by Birgitte Rubæk.

Table 8. Morphometric summary of the specimens of *Pseudostygarctus triungulatus* examined and measured in LM. Measurements in µm.

USNM no	**Holotype female 53 279**	**Paratype male 53 280**
Body length	139	101
Median cirrus	16	15
Internal cirri	16	16
External cirri	18	18
Lateral cirri	27	25
Primary clavae (length x widtht)	17 x 3	15 x 6
Secondary clavae (width x height)	10 x 7	14 x 9
Cirri E	35	43
4th leg sense organ (length x widtht)	6 3 x 5	6 4 x 8

the gonopore, an internal cuticular bar is present at the opening of the seminal receptacle duct (Figure 21B - arrow). Furthermore, an external cuticular pocket extends from the opening of the seminal receptacle duct and overlaps the gonopore (Figure 21A - arrow). The anus is sub-terminal and is closed by a three-lobed cuticular system consisting of two large lateral lobes and a small posterior lobe (Figures 21A-C). A small papilla surmounts the anterior part of the lateral lobes.

The single larva is 124 µm long from the anterior margin of the head to the base of the caudal plate and is very similar to the adult, except for the lack of gonopore and ventral plates. The lateral sheets, primary, secondary clavae, and the lateral processes of the caudal plate are of the same shape as the adult; however, they appear less developed.

Remarks: The most prominent features distinguishing *Pseudostygarctus galloae* nov. sp. from congeneric species are the sculpture of the head plate, small individualized ventral plates, and the presence of sheets to both sides of the lateral process spines and along both the anterior and the posterior margins of all body and caudal plates. Another conspicuous character is the presence of heavily ventral cuticularized branching ridges on the lateral processes, shared only by *Pseudostygarctus triungulatus*. However, the most interesting character of *P. galloae* nov. sp. is the claw number of the sexually mature specimens. The typical larval character of only two claws per leg is a clear indication of paedomorphosis. With the exception of claw number, *P. galloae* nov. sp. displays no other apparent larval/premature characters and is therefore considered neotenic. Another interesting character of *P. galloae* nov. sp. is the presence of internal cuticular bars and external cuticular pockets associated with the genital system. This feature is present in *Mesostygarctus* and, as revealed by our examination, also to be found in *Pseudostygarctus mirabilis* and *P. apuliae*. However, the configuration of the seminal receptacles of both *P. mirabilis* and *P. apuliae* is more similar to that seen in *Mesostygarctus intermedius* (see Figure 27A) than to *P. galloae*.

Pseudostygarctus triungulatus McKirdy, Schmidt & McGinty-Bayly, 1976

Diagnosis (emended). *Pseudostygarctus* with almost semi-circular head plate divided into five lobes: one medial, two medio-lateral and two lateral lobes. The primary clava is elongate, club-shaped; secondary clava semi-globular. Three body plates, each with two pairs of lateral processes, the anterior processes are very short and sharply pointed; lateral margin of body plates with narrow cuticular sheet. Ventral surface of lateral processes with heavily cuticularized branching ridges. Caudal plate with a pair of dorso-lateral triangular processes; ventral plates absent. Each leg with three claws with dorsal spurs. No sense organs present on legs I-III. Cirrus E inserted on a large lateral process.

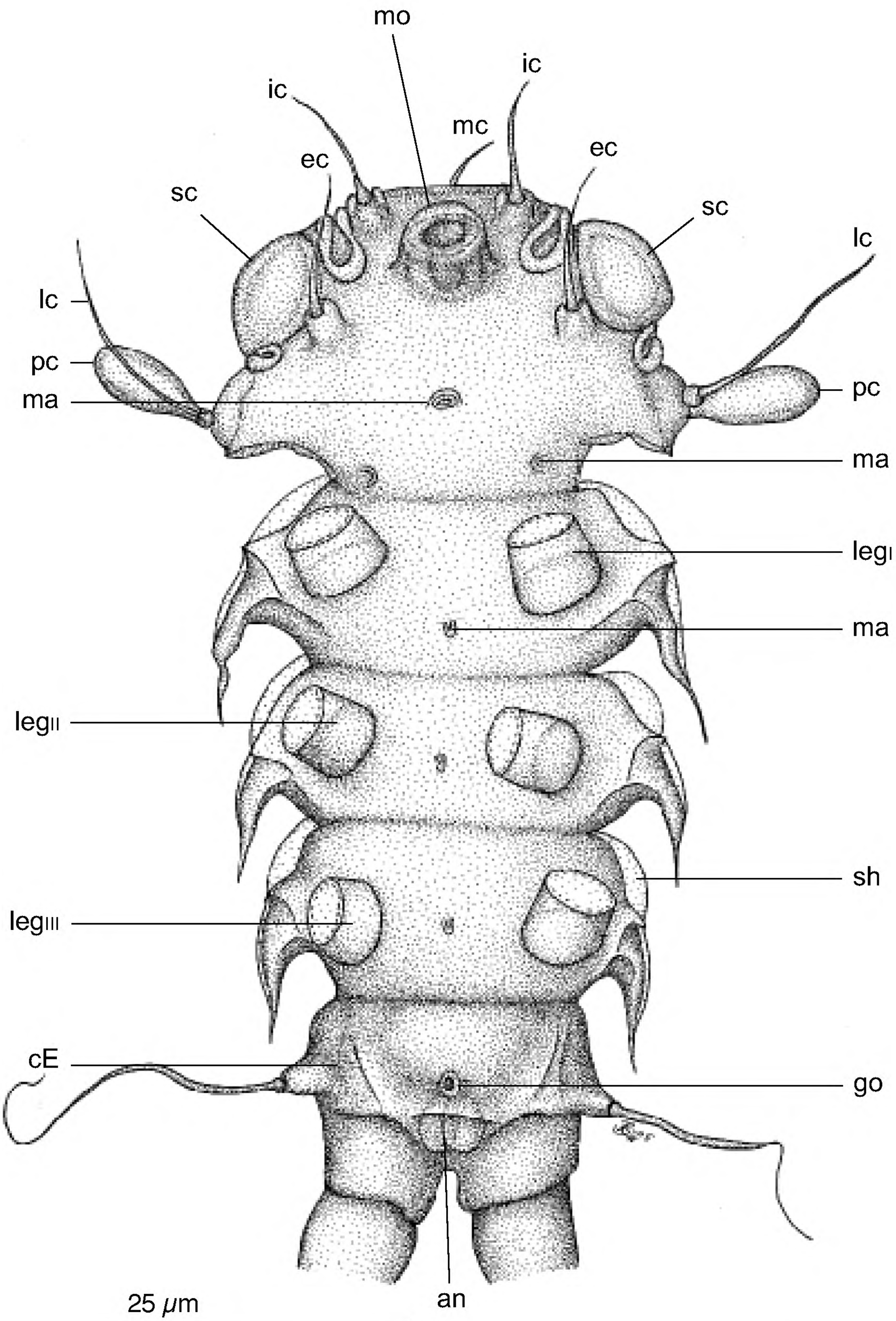


Figure 24. *Pseudostygarctus triungulatus*: adult paratypic male, ventral view. Drawing by Birgitte Rubæk.

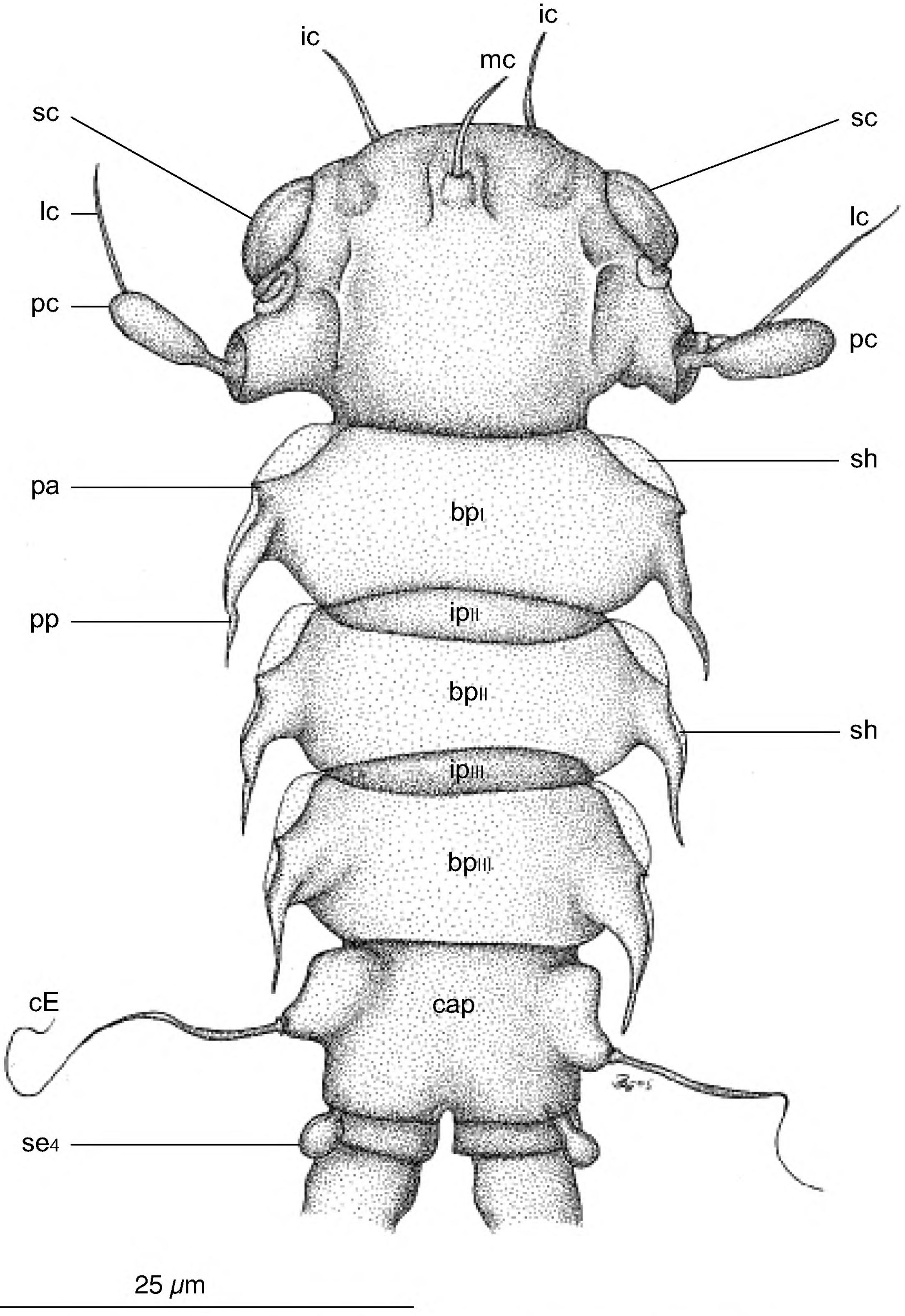


Figure 25. *Pseudostygarctus triungulatus*: adult paratypic male, dorsal view. Drawing by Birgitte Rubæk.

Material examined: Holotype, female (USNM No.53279) and one paratype, male (USNM No.53280).

The examined specimens conform closely to the original description of *Pseudostygarctus triungulatus* by McKirdy et al. (1976) in nearly all important morphological characters. However, our examination led to the recognition of several important characteristics, which adds new information to the original description of this species. Interestingly, this species displays strong secondary sexual dimorphism, which was overlooked by McKirdy et al. (1976) who described the holotype as an adult male. It is, however, an adult female. Fortunately, the single paratype included in the present examination is an adult male, and new detailed drawings as well as additional remarks on both specimens are provided in the following.

Holotype [USNM No.53279] (Figures 22 and 23, Table 8): The overall conformity to the original description is manifested in the shape of the head, caudal plate, legs and claws. Also, the cephalic sense organs agree with the original description in position and general shape. As with all other species of *Pseudostygarctus* that exhibit indentations of the head a thin cuticular membrane covers the deep lateral indentations. The three body plates each have two pairs of lateral processes. The anterior processes are very short and sharply pointed, each with a small, but well-developed semi-circular sheet. The posterior processes gradually taper and end in flexible spines. A narrow sheet runs along the lateral margin of each process, extending from the tip of the anterior process to the base of the flexible spine. The gonopore system consists of a rosette with six cells surrounded by an elevated cuticular ring. Two large and round vesicles are recognisable posterior to the gonopore. The seminal receptacle ducts are no longer recognisable, however, the opening of the genital ducts are still visible, as are the internal cuticular bars and external cuticular pockets. This clearly demonstrates the consistency of this character state in the genus.

Paratype [USNM No.53280] (Figures 24 and 25, Table 8): At 101 µm long from the anterior margin of the head to the base of the caudal plate the paratypic male is much smaller than the holotypic female (139 µm). In addition to the considerable difference in size between the female and the male, the secondary sexual dimorphism also includes the shape of the primary clavae, secondary clavae, fourth leg sense organs, and the deep indentations of the head. The primary clavae, relative to body length, are much larger in the male than the female and the shape is oval rather than elongate. The male secondary clavae (14 µm x 9 µm) and the fourth leg sense organs (8 µm x 4 µm), in spite of the smaller body size, are larger than in the female. The anterior indentations of the head are closed at the lateral margin of the head, appearing to be pressed together by the large secondary clavae. Indication of the lateral indentations of the head is present only as firmly compressed loops of thick cuticle between primary and secondary clavae. The circular male gonopore is situated anteriorly adjacent to the anus, and has a small and sharply pointed transverse cuticular bar on each side. The anus is sub-terminal and closed by two large lateral lobes.

Remarks: The only other species of *Pseudostygarctus* for which both the male and the female have been described is *Pseudostygarctus mirabilis*. This species does not display any secondary sexual dimorphism. However, in the species *P. rugosus*, where only the male is known, the atypical appearance of the primary and secondary clavae, fourth leg sense organs and the indentations of the head, are very similar to the male of *P. triungulatus*, sugesting that *P. rugosus* also displays strong secondary sexual dimorphism. Following this interpretation, we hypothesize that the females of *P. rugosus* are likely to have a pair of anterior indentations of the head (as in all other *Pseudostygarctus* species) that in the males are modified as a pair of closed rings.

Comparative morphology of the seminal receptacles

The descriptions of new species plus our re-examination of type material has led us to the recognition of several important details of the female genital structures. In order to summarize both previous and new results, and as this information is included in the present phylogenetic analyses, new detailed drawings (Figures 26-31) and additional remarks to the original description of some species are provided below.

Faroestygarctus: The detailed drawing of *Faroestygarctus dezioae* is provided to facilitate the comparison with the other genera of the subfamily from which it deviates substantially.

Mesostygarctus and *Pseudostygarctus*: In providing a more detailed description of the female genital structures of the type species *Mesostygarctus intermedius* (Figure 27A) for comparison with *M. spiralis* (Figure 27B), we recognized the presence of internal cuticular bars as well as external cuticular pockets associated with the genital system in both species. Interestingly, the internal cuticular bars and external cuticular pockets are not only shared with *Pseudostygarctus galloae* (Figure 27C) but also, as revealed by our examination, with *P. triungulatus*, *P. mirabilis* and *P. apuliae*. Furthermore, the seminal receptacles are formed as large ventral spheroid vesicles with looped ducts close to the female gonopore in all species of *Pseudostygarctus* and in *Mesostygarctus intermedius*.

Parastygarctus: When describing the larval stages of *P. sterreri*, Renaud-Mornant (1984) also gave a more detailed description of the female genital structures. The proximal part of the duct of the seminal receptacle was described as being surrounded by a distinct cuticular sheath, which opens like a funnel directed toward the gonopore. However, Renaud-Mornant did not specify whether the funnel-shaped cuticular sheath was an internal or external structure. From our examination of specimens from Bermuda and Florida it is evident that cuticular sheaths do not surround the seminal receptacle ducts (Figure 29C). Instead, the ventral cuticle is elevated, forming an external funnel-shaped cavity. The seminal receptacle duct opening protrudes from the ventral cuticle at the opening of the funnel-shaped cavity. The two cuticular funnels flanking the gonopore probably facilitate the detention and entrapment of spermatids into the ducts.

Comparing all species of *Parastygarctus* (Figures 28 and 29), the seminal receptacles conform to a general scheme, i.e., ducts of the seminal receptacles open to the exterior close to the gonopore, and extend laterally to the dorsally situated large spherical vesicles where the ducts enter from the ventral side. The only

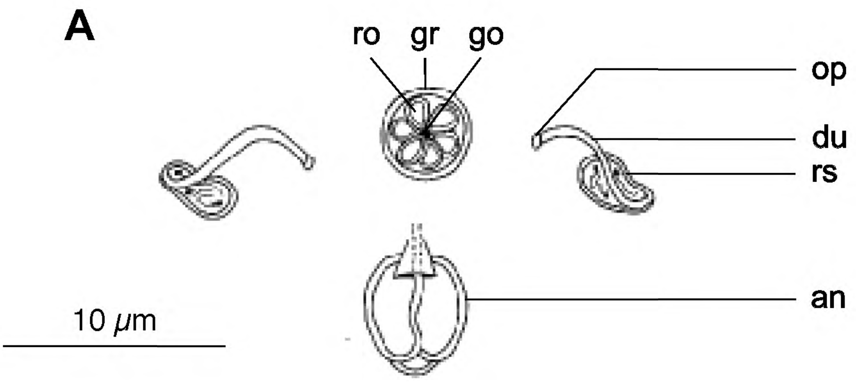
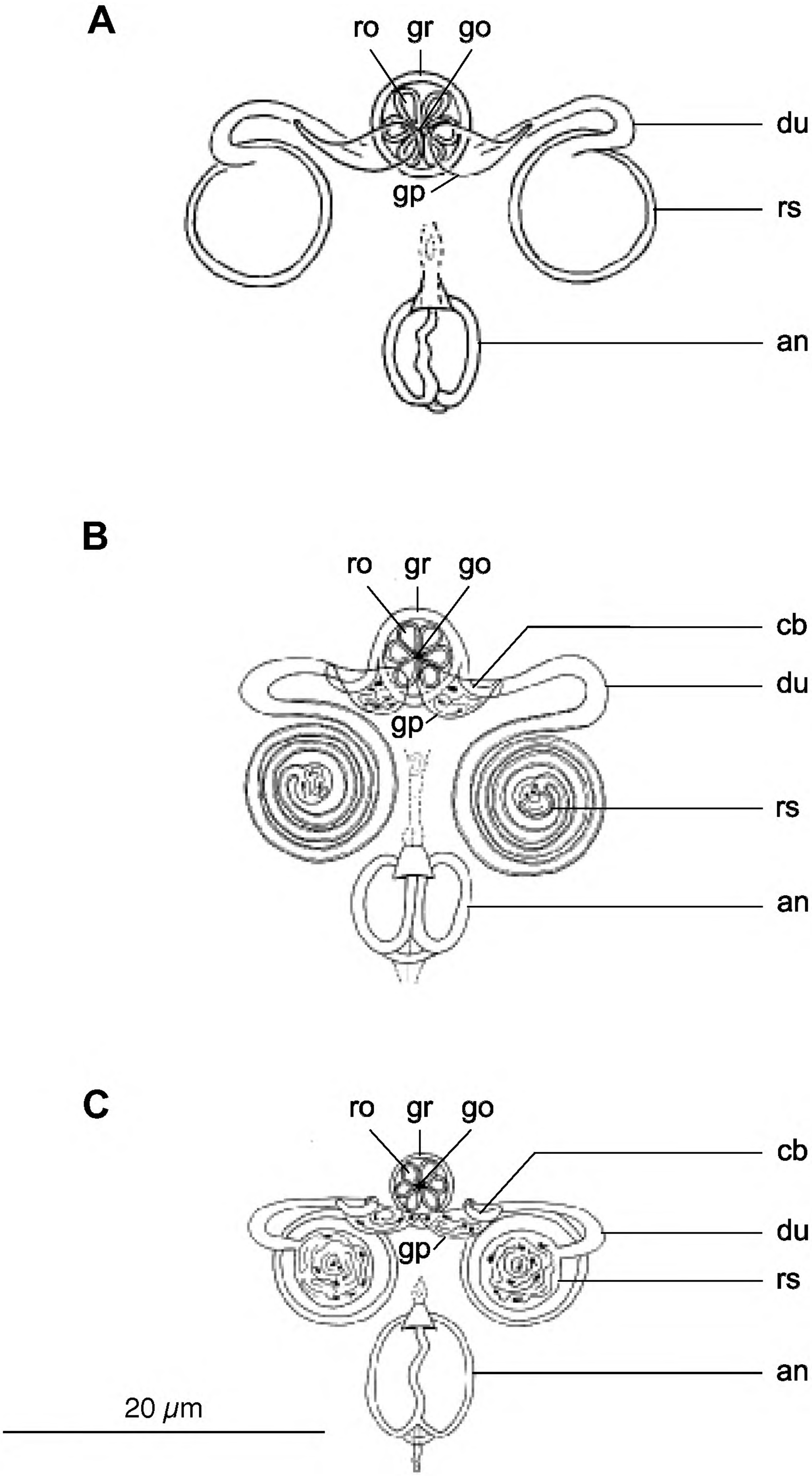


Figure 26. Detailed diagram of the genital structures: *Faroestygarctus dezioae* nov. sp.

Figure 27. Detailed diagram of the genital structures: A. *Mesostygarctus intermedius*. B. *Mesostygarctus spiralis* nov. sp. C. *Pseudostygarctus galloae* nov. sp. Drawings by Stine B. Elle.



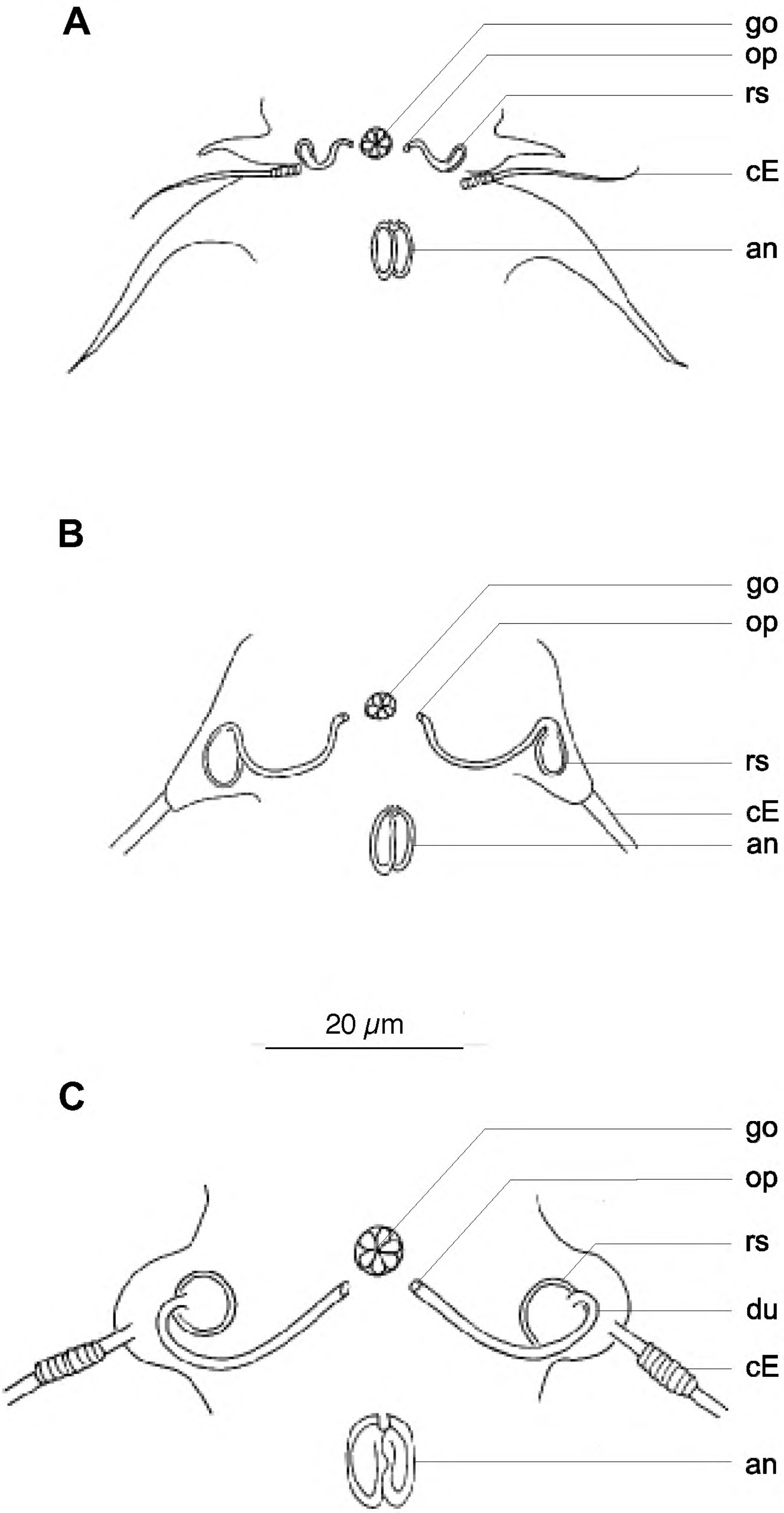
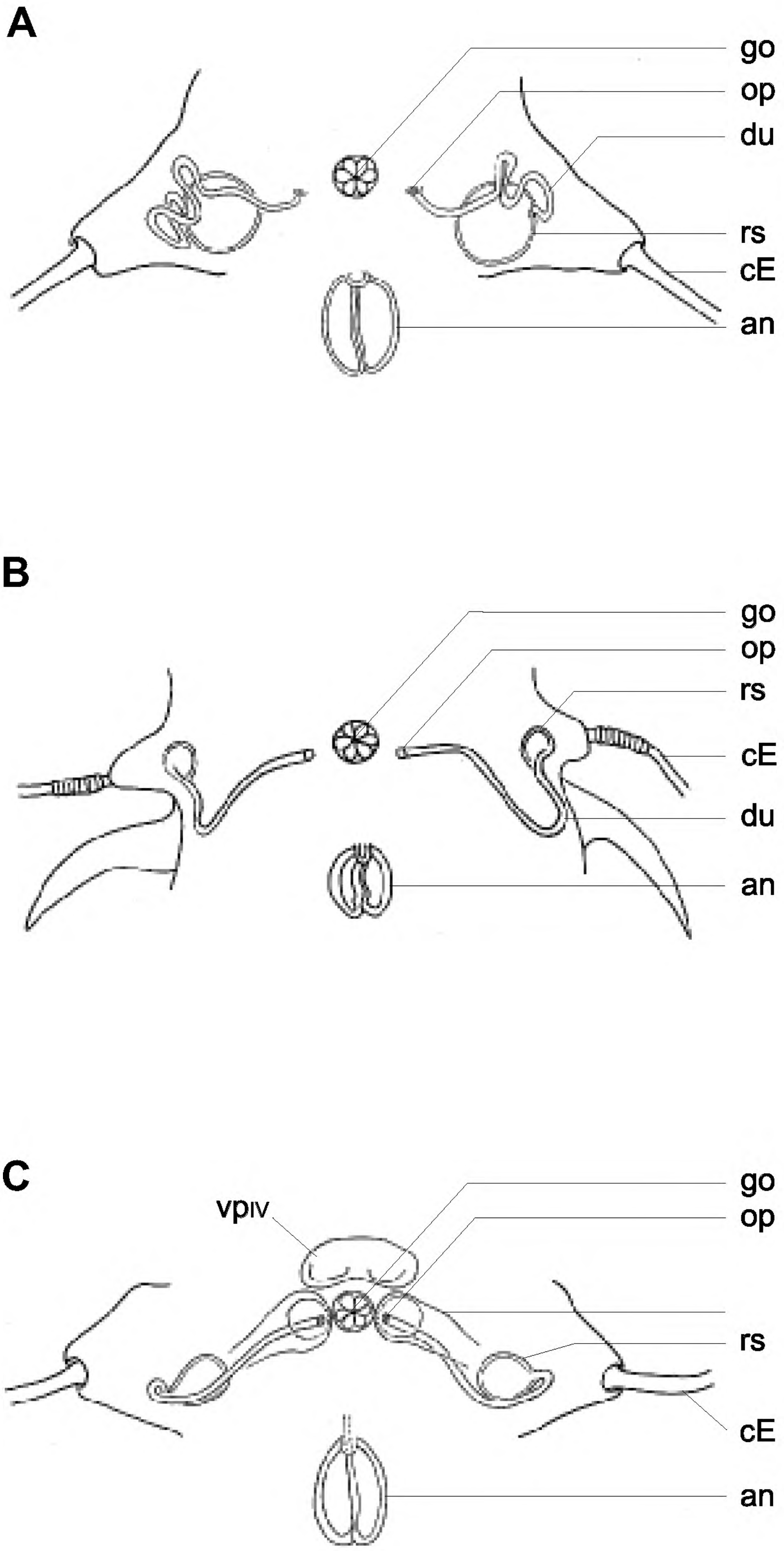


Figure 28. Detailed diagram of the genital structures: A. *Parastygarctus biungulatus* (redrawn from Morone De Lucia et al. 1984). B. *Parastygarctus higginsi* (redrawn from Renaud-Mornant 1967). C. *Parastygarctus renaudae* (redrawn from Grimaldi de Zio et al. 1987).

Figure 29. Detailed diagram of the genital structures: A. *Parastygarctus robustus* nov. sp. B. *Parastygarctus svennevigi* nov. sp. C. *Parastygarctus sterreri*. Drawings by Stine B. Elle.



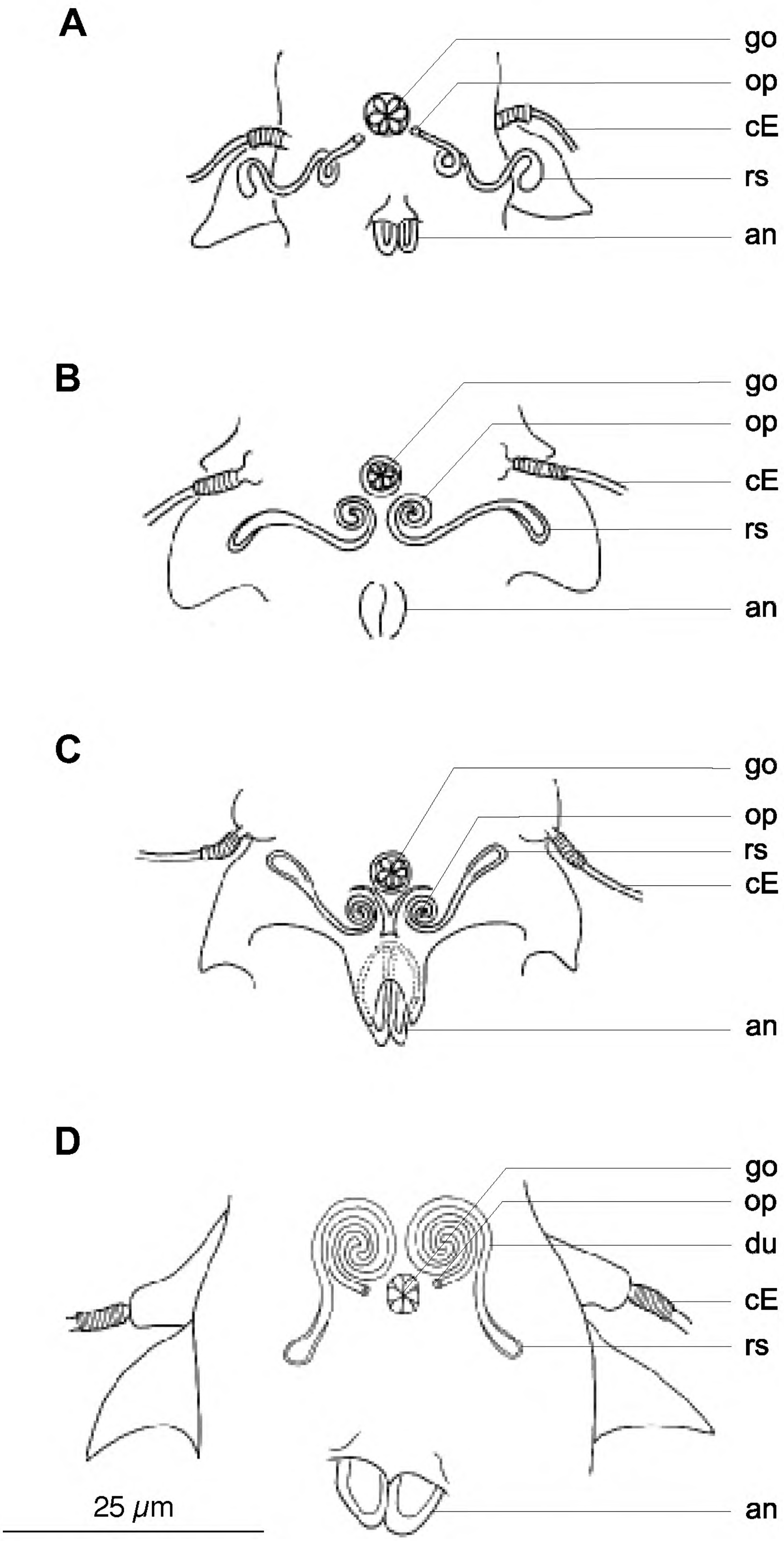


Figure 30. Detailed diagram of the genital structures: A. *Stygarctus bradypus* (redrawn from Renaud-Mornant 1970). B. *Stygarctus lambertii* (redrawn from Grimaldi de Zio et al. 1987). C. *Stygarctus gourbaultae*. D. *Stygarctus spinifer*.

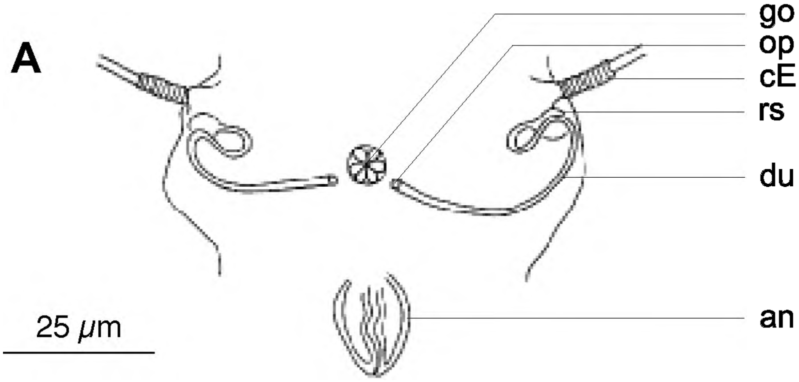


Figure 31. Detailed diagram of the genital structures: *Stygarctus granulatus* (redrawn from Pollock 1970).

exception to this scheme, which is probably due to its paedomorphic origin, is in the neotenic species *P. biungulatus* (Figure 28A) where the vesicle is a small ventrally situated enlargement of the terminal end.

Stygarctus: In the original description of *Stygarctus spinifer*, Hiruta (1985) illustrated the configuration of the seminal receptacles of a paratypic female but did not add any remarks about these structures. Following the re-examination of Hiruta's type material, we discovered some interesting new details. Each seminal receptacle duct is coiled into a complex double spiral, anterior to the gonopore (Figure 30D). From the exterior opening of the ducts, laterally to the gonopore, the tubes curve upwards and inwards, towards the centre of a spiral, then reverse direction, coiling outwards and away from the spiral, to terminate in a small vesicle, posterior to the gonopore.

Comparing all species of *Stygarctus* (Figures 30 and 31), the seminal receptacles conform to a general scheme, i.e., the ducts of the seminal receptacles open to the exterior close to the gonopore, and extend laterally, describing a complete loop, before they terminate in a small ventro-lateral vesicle. The medio-lateral position of the vesicles of *S. granulatus* (Figure 31A), rather than in a ventro-lateral position, is the only slight deviation from the general scheme.

Phylogenetic analysis

Character states

A character state that unambiguously defines a taxon on the generic level has been marked with the taxon name in the character list (Appendix 1). A brief description or discussion has been added to the characters where appropriate. Inapplicable characters have been coded as missing data to prevent overweighting.

Most of the cuticular plate characters have been coded as inapplicable in the unarmoured *Coronarctus verrucatus*. A new character state "dorsal plates secondarily reduced" was introduced to accommodate *M. gerdae*, which clearly belongs to the genus *Megastygarctides* (see below). The presence in *M. gerdae* of a ventral cephalic plate supports our interpretation that the absence of body plates is a secondarily derived condition. Without the new character state the cuticular plate characters for *M. gerdae* would have been coded as inapplicable, which by creating too many missing value character states might have had a topological effect on the tree (Maddison 1993).

Clades, clade support (all analyses) and character tracing

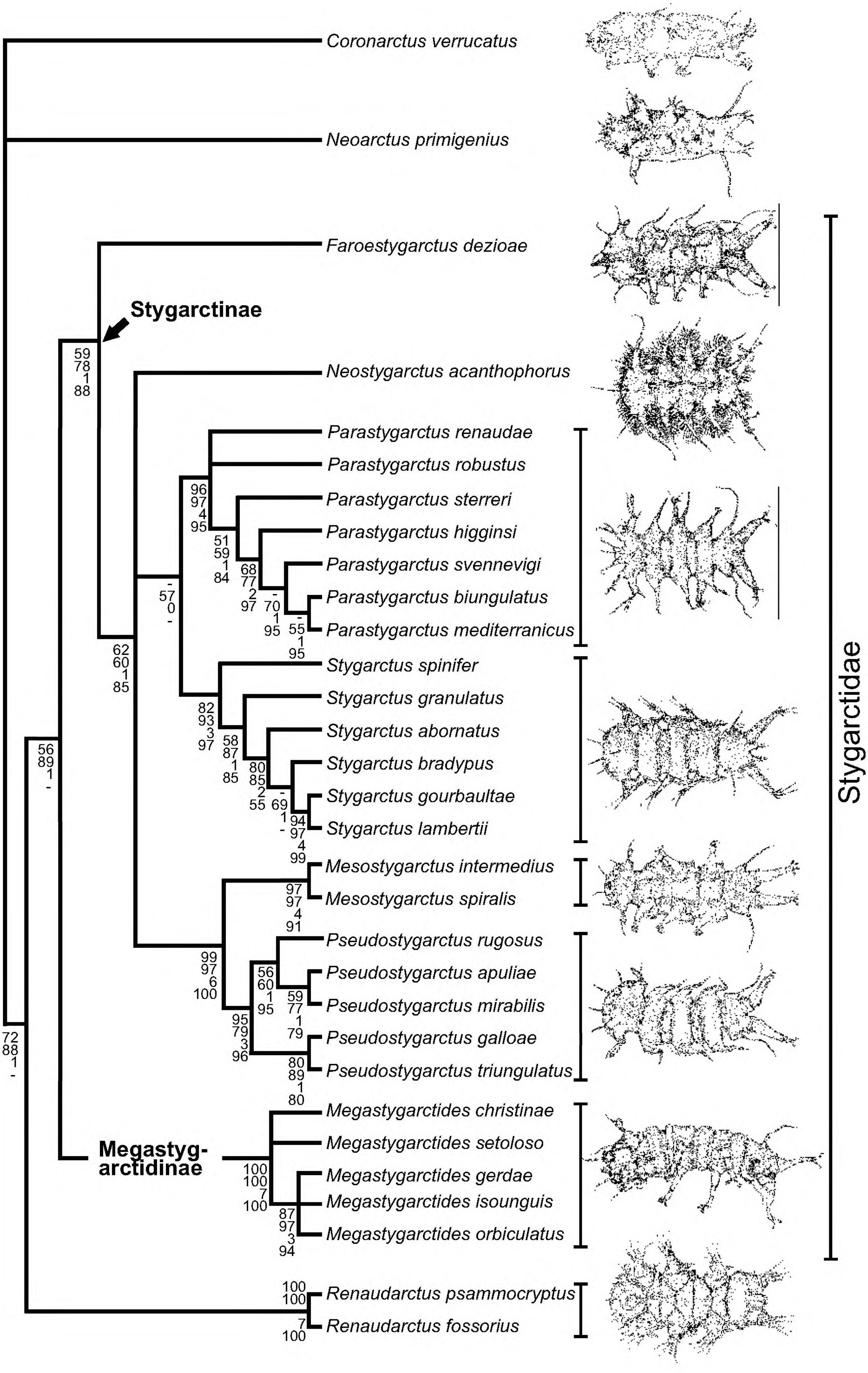
In the analyses of the complete data matrix (Figures 32 and 33) the maximum parsimony (MP) analyses resulted in a higher basal resolution than the Bayesian inference (BI) analysis. Both methods inferred the monophyly of the different genera and had identical intrageneric topologies, differing only with respect to weakly supported nodes.

In the section below we present the most notable results from the character tracing of the major clades in figure 32. Focus will be on synapomorphies and homoplasies (convergent evolution and reversals). Equivocal character tracing (uncertain character state designation to the stem of a clade) regarding the synapomorphic character states will be mentioned. Reference to the character and character state is given using the following notation 1(0), i.e. character 1, character state 0. Overall branch support is given in the notation (bootstrap, successive weighting bootstrap, Bremer index and posterior probability). Statements regarding the tree topology are based on the 50% majority rule consensus tree resulting from the MP analysis using successive weighting. This tree was chosen to represent the analyses as it has the highest basal resolution and branch support.

Intrageneric relationships: All genera remained monophyletic in the phylogenetic analyses despite successive weighting, changes in outgroups and inference method. The ranking of the overall support results in: *Renaudarctus* (100, 100, 7, 100), *Megastygarctides* (100, 100, 7, 100), *Mesostygarctus* (97, 97, 4, 91), *Parastygarctus* (96, 97, 4, 95), *Stygarctus* (82, 93, 3, 97) and *Pseudostygarctus* (95, 79, 3, 96).

The monophyly of *Renaudarctus* received high support (100, 100, 7, 100) and support from 15 character states: 12(1) presence of a dorsal leg plate; 21(1) the sculpture of the third intersegmental plate with median narrowing (also present in *Stygarctus* except *S. granulatus*); 25(1) large plate not following the shape of the head (also present in *Megastygarctides christinae* and *M. gerdae*); 26(1) presence of ventral body plates (also evolved in *Mesostygarctus*, *Pseudostygarctus* [except *P. triungulatus*], *Parastygarctus renaudae* and *Stygarctus*); 40(1) the presence of two lateral processes of the caudal plate (also present in the clades of (*Pseudostygarctus gal-*

Figure 32. The phylogeny of Stygarctidae inferred by maximum parsimony (MP) with the characters reweighted using the rescaled consistency index. The morphology of the different genera is illustrated using small icons. The values of node support are unreweighted bootstrap, reweighted bootstrap, Bremer support and posterior probability as a percentage.


Coronarctus verrucatus
Neoarctus primigenius
Faroestygarctus dezioae
Stygarctinae
59 78 1 88
Neostygarctus acanthophorus
Parastygarctus renaudae
Parastygarctus robustus
96 97 4 95
Parastygarctus sterreri
Parastygarctus higginsi
51 59 1 84
Parastygarctus svennevigi
68 77 2 97
- 57 0 -
Parastygarctus biungulatus
- 70 1 95
Parastygarctus mediterranicus
- 55 1 95
62 60 1 85
Stygarctus spinifer
Stygarctus granulatus
82 93 3 97
Stygarctus abornatus
58 87 1 85
Stygarctus bradypus
80 85 2 55
Stygarctus gourbaultae
- 69 1 -
Stygarctus lambertii
94 97 4 99
56 89 1 -
Mesostygarctus intermedius
Mesostygarctus spiralis
97 97 4 91
Pseudostygarctus rugosus
99 97 6 100
Pseudostygarctus apuliae
56 60 1 95
Pseudostygarctus mirabilis
59 77 1 79
95 79 3 96
Pseudostygarctus galloae
Pseudostygarctus triungulatus
80 89 1 80
72 88 1 -
Megastygarctides christinae
Megastyg-arctidinae
Megastygarctides setoloso
100 100 7 100
Megastygarctides gerdae
Megastygarctides isounguis
87 97 3 94
Megastygarctides orbiculatus
Stygarctidae
100 100 7 100
Renaudarctus psammocryptus
Renaudarctus fossorius

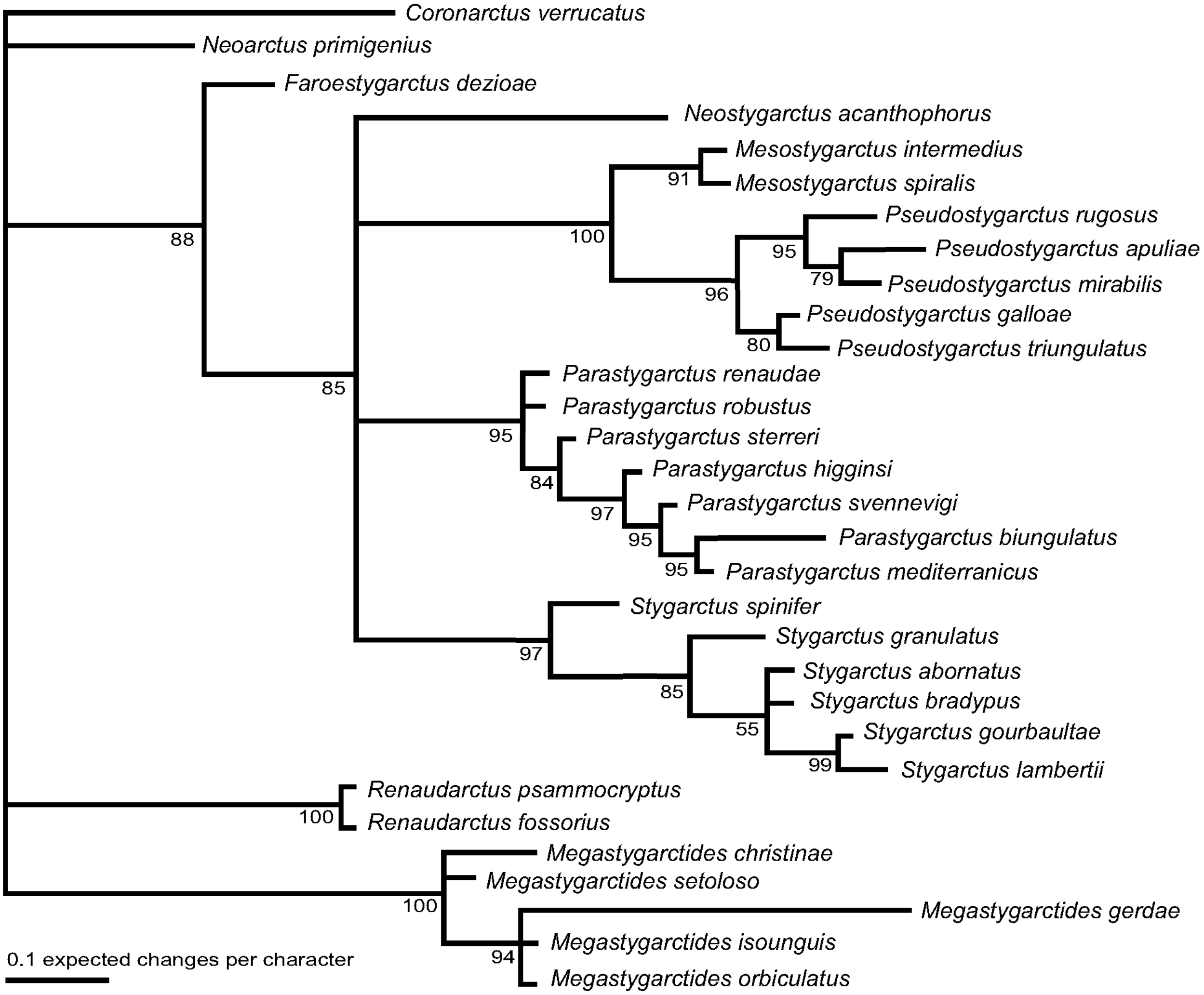


Figure 33. The phylogeny of Stygarctidae inferred by Bayesian inference (BI). The branch support is posterior probability as a percentage and the branch lengths illustrate the character divergence of the clades and species.

loae, *P. triungulatus*), ((*Parastygarctus biungulatus*, *P. mediterranicus*), *P. svennevigi*), and *Stygarctus* [except *S. granulatus*]; 42(1) caudal spikes (also present in *Parastygarctus biungulatus* and *Stygarctus* [except *S. spinifer*]); 44(2) the vesicle of the seminal receptacle is round and approximately the same size as the gonopore (also present in *Neostygarctus acanthophorus*); 54(2) the claws insert via toes on the foot (also present in *N. acanthophorus*); 55(1) the dorsal accessory of the median claws are long thin filaments (also present in *Parastygarctus* and *Stygarctus*); 58(2) claws not j-shaped, consisting of a strongly cuticularized portion and a thin, more translucent laminar portion (also present in *N. acanthophorus*); 60(2) the secondary clavae are "flattened" sausage-shaped (also present in *Megastygarctides christinae*); 64(1) the median cirrus is located anterior on the cephalic plate, not posterior to the incision between the internal and external cirri (also present in *N. acanthophorus*, and the Mediterranean clade of *Pseudostygarctus*); 67(0) the external cirri are located frontal on the head (also evolved in *N. acanthophorus* and the genus *Parastygarctus*); 78(2) a ventral mouth (also present in *N. acanthophorus*, *Pseudostygarctus* [except *P. mirabilis*] and the clade (*Stygarctus bradypus*, (*S. gourbaultae*, *S. lambertii*)); 80(1) the bifurcating stylet furcae are pointed posteriorly (also present in *N. acanthophorus*). All the other species mentioned above have similar character states that appear to have evolved by convergent evolution. However, of particular note is the high degree of convergence between *Renaudarctus* and *Neostygarctus* (the eight character states 44(2), 54(2), 55(1), 58(2), 64(1), 67(0), 78(2) and 80(1)), which might indicate a closer phylogenetic relationship than inferred by the present analyses

The monophyly of *Megastygarctides* received high support (100, 100, 7, 100) and support from 14 character states: 9(2) the head is extended anterior-posteriorly; 10(0) the absence of pillars in the cuticle (also absent from *Coronarctus* and *Mesostygarctus*), 14(1) the body plates and intersegmental plates are of equal thickness (except in *M. gerdae* where the dorsal body plates are secondarily reduced); 16(1) the presence of intersegmental plate m1 (except *M. gerdae*; also present in *Pseudostygarctus apuliae*); 17(1) the presence of intersegmental plate m4 (except *M. gerdae*; also present in *Pseudostygarctus apuliae* and *Parastygarctus biungulatus*); 18(1) the dorsal intersegmental plates are large (except *M. gerdae*); 19(3) the presence of four intersegmental plates (also present in *Pseudostygarctus apuliae*; *Megastygarctides christinae* has developed an extra intersegmental plate and *M. gerdae* has secondarily reduced all dorsal plates); 20(0) the absence of sculpture on intersegmental plate m1 (except *M. gerdae*; also absent from *Parastygarctus higginsi*, *P. mediterranicus*, *P. sterreri* and *P. svennevigi*); 28(0) the absence of lateral processes of the body plates but the basal relationship is equivocal (except *M. gerdae*; also absent from *Neoarctus*); 44(4) the vesicle of the seminal receptacle is a large pouch (also evolved in *Coronarctus* and not scored in *Megastygarctides isounguis* and *M. setoloso*); 51(1) presence of a complex external genital cuticular structure (not scored in *Megastygarctides isounguis* and *M. setoloso*); 53(3) four claws on the first three pairs of legs, two on the last pair; 54(1) claws originate from a short pedestal; 57(2) claws of different size between each pair of legs. A single unresolved internal clade receiving high-intermediate branch support (87, 97, 3, 94) was inferred consisting of *M. gerdae*, *M. isounguis* and *M. orbiculatus*. The five character states that supported this clade were: 2(1) the head has four lobes; 3(4) the anterior lobes of the head are more protruded than the lateral lobes; 47(0) the opening of the seminal receptacle overlap the gonopore (not scored in *M. isounguis* and also present in the clade (*Mesostygarctus*, *Pseudostygarctus*)); 71(1) the internal cirrus, external cirrus and secondary clavae are located on the same head lobe; 72(1) presence of a deep incision between internal cirri.

The monophyly of *Mesostygarctus* received high support (97, 97, 4, 91) and support from eight character states: 10(0) the absence of pillars in the cuticle (also absent from *Coronarctus verrucatus* and as a synapomorphy of the *Megastygarctides* clade); 25(2) large ventral cephalic plate following the shape of the head (also present as a synapomorphy of the *Stygarctus* clade); 27(1) the presence of ventral segmental cuticular folds; 30(5) the lateral processes are two similar posterior processes; 33(2) the two lateral processes are arranged latero-ventral and latero-dorsal; 35(0) the posterior process of the body plates is short and gradually tapering (also present as synapomorphies of *Renaudarctus* and *Stygarctus* [except *S. spinifer*]; 37(2) sheets present only on the dorso-lateral margin of the body plates (not associated with the ventro-lateral processes); 59(3) the primary clavae are elongate with spine-like termination (also present in *Pseudostygarctus galloae* and *P. triungulatus*, but the character tracing is equivocal).

The monophyly of *Parastygarctus* received high support (96, 97, 4, 95) and support from eight character states: 3(2) head with all lobes greatly protruded to about the same extent; 4(2) a deep incision between internal and external cirri; 9(1) the head has a large "neck" extension (also present in *Neostygarctus acanthophorus*); 35(1) the posterior process of the body plates is long and gradually tapering (also present in *N. acanthophorus* and *Stygarctus spinifer*, but the character tracing is equivocal); 45(2) the vesicle of the seminal receptacle is located dorso-laterally; 59(0) pedunculate and strongly elongate club-shaped primary clavae (except in the clade (*Parastygarctus biungulatus*, *P. mediterranicus*)); 67(0) the external cirri are located frontally on the head (also in *Renaudarctus* spp. and *N. acanthophorus*);

69(1) secondary clavae situated posterior to the external cirri; 74(0) cirrus E tripartite comprising smooth proximal, accordion articulation and flagellum except the clade ((*Parastygarctus biungulatus*, *P. mediterranicus*), *P. svennevigi*), and also present in *N. acanthophorus*); 75(1) the cirrus E is placed on a dorso-lateral process (except *Parastygarctus biungulatus*; and though present in *N. acanthophorus* and *Megastygarctides* the character tracing is equivocal); 80(2) bifurcate stylet furcae bent anteriorly (not scored for *P. biungulatus* and *P. mediterranicus*); 81(1) the pharyngeal bulb reaches further than the first body segment (not scored for *P. biungulatus* and *P. robustus*). The internal phylogenetic relationships of *Parastygarctus* species received low-intermediate support by the bootstrap analysis, with Bremer support values of 1-2, but several significant support (> 95) posterior probability values from the BI analysis.

The monophyly of *Stygarctus* received high to intermediate support (82, 93, 3, 97) and support from seven characters states: 4(1) moderate incision between internal and external cirri (also in *Neostygarctus acanthophorus*); 6(1) the presence of a lateral lobe with a posterior sheet; 21(1) median narrowing of the third intersegmental plate (m3) (the character tracing is equivocal, *Stygarctus granulatus* has no median narrowing and a median narrowing is also present in *Renaudarctus* spp.); 25(2) large ventral cephalic plate following the shape of the head (also in *Mesostygarctus* spp.); 40(1) the presence of two pairs of lateral processes on the caudal plate (except *S. granulatus*, and also present in *Renaudarctus*, and the clades ((*Parastygarctus biungulatus*, *P. mediterranicus*), *P. svennevigi*) and (*Pseudostygarctus galloae*, *P. triungulatus*); 44(0) the vesicle of the seminal receptacle is a small enlargement of the terminal end (also in *Parastygarctus biungulatus*); 75(3) cirrus E is placed on a small ventro-lateral process.

Stygarctus spinifer was inferred as the sister-group to the other *Stygarctus* species. The five remaining species, (*S. granulatus*, (*S. abornatus*, (*S. bradypus*, (*S. gourbaultae*, *S. lambertii*)))), formed an overall low supported clade (58, 87, 1, 85). However, this clade is supported by nine character states: 30(0) a single, more or less funnel-shaped, lateral process of the body plates (the clade (*S. gourbaultae*, *S. lambertii*) has two lateral processes); 31(1) the presence of lateral funnel-shaped processes; 32(0) the funnel-shaped lateral processes are without anterior spines (anterior spines are present in the clade (*S. gourbaultae*, *S. lambertii*)); 34(1) termination of the anterior process as a single point (also in *Mesostygarctus intermedius*, *Pseudostygarctus rugosus* and the clade (((*Parastygarctus biungulatus*, *P. mediterranicus*), *P. svennevigi*), *P. higginsi*)); 35(0) short, gradually tapering posterior processes of the body plates (also in *Mesostygarctus* spp., but the character tracing is equivocal); 36(1) the presence of body plate lateral sheets (also present in the clade (*Mesostygarctus*, *Pseudostygarctus*)); 37(0) sheets only present terminally on the funnel-shaped ventro-lateral processes; 42(1) the presence of caudal spikes (also in *Parastygarctus biungulatus* and *Renaudarctus* spp.); 45(0) the vesicle of the seminal receptacle is ventro-lateral (also in *Renaudarctus* spp., *Neostygarctus acanthophorus* and *Faroestygarctus dezioae*).

The monophyly of *Pseudostygarctus* received intermediate support (95, 79, 3, 96) and support from nine character states: 5(1) a spine is present on the lateral lobe of the head (except *Pseudostygarctus rugosus*); 7(1) the presence of a frontal sheet on the head (absent in *P. apuliae*); 8(1) the presence of a sheet covering the indentation of the lateral lobe anterior to the lateral cirrus and primary clava (absent in *P. apuliae*); 30(4) two lateral processes one of which ends in a long flexible spine; 33(0) the lateral processes are arranged in the same dorso-ventral level (also in *Stygarctus gourbaultae*); 35(2) the posterior process of the body plates end in a long flexible spine (also in *Faroestygarctus dezioae*); 37(1) sheets present along the margin of the lateral processes; 73(1) "ball and socket" insertion of cirrus E; 74(2) cirrus E is a long tapering spine. 78(2) the mouth is ventral (except *Pseudostygarctus mirabilis*, present in *Renaudarctus* spp., *Neostygarctus acanthophorus*, and the clade (*Stygarctus bradypus*, (*S. gourbaultae*, *S. lambertii*))). Within *Pseudostygarctus* a low supported Mediterranean clade (56, 60, 1, 95) consisting of (*P. rugosus*, (*Pseudostygarctus apuliae*, *P. mirabilis*)) was inferred. The Mediterranean clade is supported by the following three character states: 38(1) large lateral sheets on the body plates; 59(1) the primary clavae are pedunculate and moderately elongated club-shaped (the character tracing is equivocal and this character state is also present in *Megastygarctides*, *Stygarctus* [except *S. lambertii*] and in the clade (*Parastygarctus biungulatus*, *P. mediterranicus*); 64(1) the median cirrus is located anterior on the cephalic plate, not posterior to the incision between the internal and external cirri (also in *Neostygarctus acanthophorus*, and *Renaudarctus* spp.).

Intergeneric relationships: *Mesostygarctus* and *Pseudostygarctus* were inferred to be sister-groups. The clade received high support (99, 97, 6, 100) and support from ten character states: 4(3) the compact head is inserted directly on the body (except *P. rugosus* where the head is not fused with scapular plate); 29(1) two lateral processes of the body plates (also present in the clades (((*Parastygarctus biungulatus*, *P. mediterranicus*), *P. svennevigi*), *P. higginsi*) and (*Stygarctus gourbaultae*, *S. lambertii*)); 36(1) the presence of body plates lateral sheets (also in *Stygarctus* [except *S. spinifer*]); 44(3) the vesicle of the seminal receptacle is round and larger than the gonopore (except *Mesostygarctus spiralis* where the vesicle is a large round spiral; 47(0) the opening of the seminal receptacle duct overlap the gonopore (also in *Megastygarctides gerdae* and *M. orbiculatus*); 48(0) the loop of the duct is close to the vesicle of the seminal receptacle (also evolved in *Parastygarctus robustus*, *Stygarctus granulatus* and *Neostygarctus acanthophorus*); 49(1) presence of cuticular bars at the opening of the seminal receptacle duct; 50(1) presence of cuticular pockets at the opening of the seminal receptacle duct; 59(3) the primary clavae are elongate with spine-like termination (except in the Mediterranean *Pseudostygarctus* clade, and the character tracing is equivocal); 74(2) cirrus E is a long tapering spine; 75(2) cirrus E is located on the end of a large lateral process.

Parastygarctus and *Stygarctus* were inferred to be sister-groups with low branch support (-, 57, 0, -). The sister-group relationship is supported by seven character states: 6(1) the presence of a posterior spine on the lateral lobe of the head (also present in *Pseudostygarctus* [except *P. rugosus*] and the character tracing is equivocal); 40(1) two pairs of lateral processes (a single pair present in *P. higginsi*, *P. renaudae* and *S. bradypus*, and two pairs also present in the clade (*Pseudostygarctus galloae*, *P. triungulatus*) and *Renaudarctus* spp.); 55(1) the dorsal accessory of the median claw is a long thin filament (also in *Renaudarctus* spp.); 57(0) claws on the first three pairs of legs of approximately the same size with the claws on the fourth pair slightly larger; 60(0) the secondary clavae are elongate club-shaped; 61(0) primary and secondary clavae are similar in shape (except *S. lambertii* and also present in *Neoarctus primigenius*); 62(0) erect elongate club-shaped secondary clavae (except the internal clade (*S. bradypus* (*S. abornatus* (*S. gourbaultae*, *S. lambertii*))) which has the secondary clavae bent along the frontal lobe. Note that the character is non-applicable outside the clade (*Parastygarctus*, *Stygarctus*) because elongate club-shaped secondary clavae are absent).

Higher-level relationships: The MP analysis inferred unresolved relationships between (*Mesostygarctus*, *Pseudostygarctus*), (*Parastygarctus*, *Stygarctus*) and *Neostygarctus* whereas the BI analysis inferred unresolved relationships between *Neostygarctus*, *Parastygarctus*, *Stygarctus*, and (*Mesostygarctus*, *Pseudostygarctus*). Both methods inferred a sister-group relationship of *Faroestygarctus dezioae* with the stygarctinae genera (including *Neostygarctus*). In the MP analyses *Megastygarctides* was the sister-group to all the above mentioned taxa and *Renaudarctus* was inferred to be the sister-group to Stygarctidae (including Neostygarctidae), but this relationship between Stygarctinae, Megastygarctinae and Renaudarctidae was unresolved in the BI analysis.

The MP analysis inferred the phylogenetic position of *Faroestygarctus dezioae* to be basal within Stygarctinae, as sister-group to the rest of the Stygarctinae including *Neostygarctus*; though this relationship received low support (59, 78, 1, 88). The seven character states supporting this clade were: 3(0) all head lobes are moderately protruded to about the same extent (except in *Parastygarctus* were all lobes are greatly protruded and *Neostygarctus* were the lateral lobes are greatly protruded); 9(0) the head is almost semi-circular (except in *Parastygarctus* and *Neostygarctus* were the head has a large "neck" extension); 11(1) the outline of body cross section is dorso-ventral flattened; 28(1) the presence of lateral processes of the body plates (the character tracing is equivocal and lateral processes are also present in *Renaudarctus* spp.); 56(0) claw accessories only on medial claws (also in *Coronarctus* and on all claws in *Pseudostygarctus triungulatus*); 68(0) the primary clava is posterior to the lateral cirrus; 79(0) the placoids in the pharyngeal bulb have internal stylet support (internal stylet supports are missing in *Neostygarctus* and this pharyngeal bulb character has only been scored for 9 taxa of the 22 taxa in the clade; furthermore this character tracing is equivocal, i.e. no definitive character state could be assigned to many of the clades). The BI analysis inferred a clade constituted of the same taxa but with an incongruent topology.

In a low supported clade (56, 89, 1, -) Megastygarctidinae was inferred to be the sister-group to an expanded Stygarctinae that included *Faroestygarctus dezioae* and *Neostygarctus*. The six character states supporting this clade were: 1(1) head differentiated in lobes; 40(0) one pair of lateral processes on the caudal plate (two pairs of lateral processes are present in *Pseudostygarctus triungulatus*, *P. galloae*, in *Parastygarctus* [except for *P. higginsi* and *P. renaudae*] and in *Stygarctus* [except for *S. bradypus*], and *Megastygarctides gerdae* has secondarily reduced all plates. The character tracing was equivocal); 58(1) the claws are j-shaped without basal spur (also in *Neoarctus* and the claws are not j-shaped, consisting of a strongly cuticularized portion and a thin, more translucent laminar portion in *Neostygarctus* and *Renaudarctus* spp.); 63(0) the absence of tertiary clavae; 66(0) the internal cirri are inserted on a distinct head lobe; 75(1) cirrus E is located on a dorso-lateral process (except in *Faroestygarctus dezioae* and *Parastygarctus biungulatus* where it is not located on a process, in the clade (*Mesostygarctus*, *Pseudostygarctus*) where it is located on at the end of a large lateral process, and *Stygarctus* were it is located on a small ventro-lateral process). This clade was not inferred by the BI analysis.

A low supported clade (72, 88, 1, -) placed Renaudarctidae as the sister-group to an expanded Stygarctidae including Neostygarctidae. The six characters supporting this clade were: 13(2) the presence of both segmental and intersegmental plates (except in *Neostygarctus acanthophorus* with only segmental plates and *Megastygarctides gerdae* with the plates secondarily reduced); 15(1) the presence of intersegmental plates (except in *Neostygarctus acanthophorus* with no intersegmental plates and *Megastygarctides gerdae* with the plates secondarily reduced); 46(0) the opening of the seminal receptacle duct is close to the gonopore; 65(0) internal cirri located frontal on the latero-frontal edge of the head (except *Neostygarctus acanthophorus* where it is slightly ventral on the head); 76(1) the presence of leg sense organs only on the fourth pair of legs; 77(0) the sense organ on the fourth leg is a spherical papilla (except for *Neostygarctus acanthophorus* that has an elongate papilla with pointed termination, and a pedunculate papilla with rounded termination has developed in *Megastygarctides gerdae*, *Mesostygarctus*, *Pseudostygarctus* [except *P. mirabilis*], *Parastygarctus* and *Stygarctus abornatus*, *S. bradypus* and *S. gourbaultae*. The character state in *P. mirabilis* represents subsequent reversal to the spherical papilla).

The effect of the successive weighting in the parsimony analyses: Successive weighting resulted in a single topological change implying a sister-group relationship between *Parastygarctus* and *Stygarctus* in the trees inferred from the complete data matrix. In the analyses including *Renaudarctus* spp. as the only outgroups, successive weighting did not result in any topological changes in the cladogram.

The effect of taxon removal: The analyses with various outgroup and ingroup taxa removed from the data matrix resulted in very similar topologies (not shown). The most important changes in the MP analyses occurred when removing the outgroups *Coronarctus* and

Figure 34. The phylogeny of Stygarctidae inferred by maximum parsimony with the character reweighted (MP; left) and Bayesian inference (BI; right) with *Renaudarctus* spp. as the only outgroups. The support values are unreweighted bootstrap, bootstrap and Bremer support for MP and posterior probability as a percentage (BI, right).

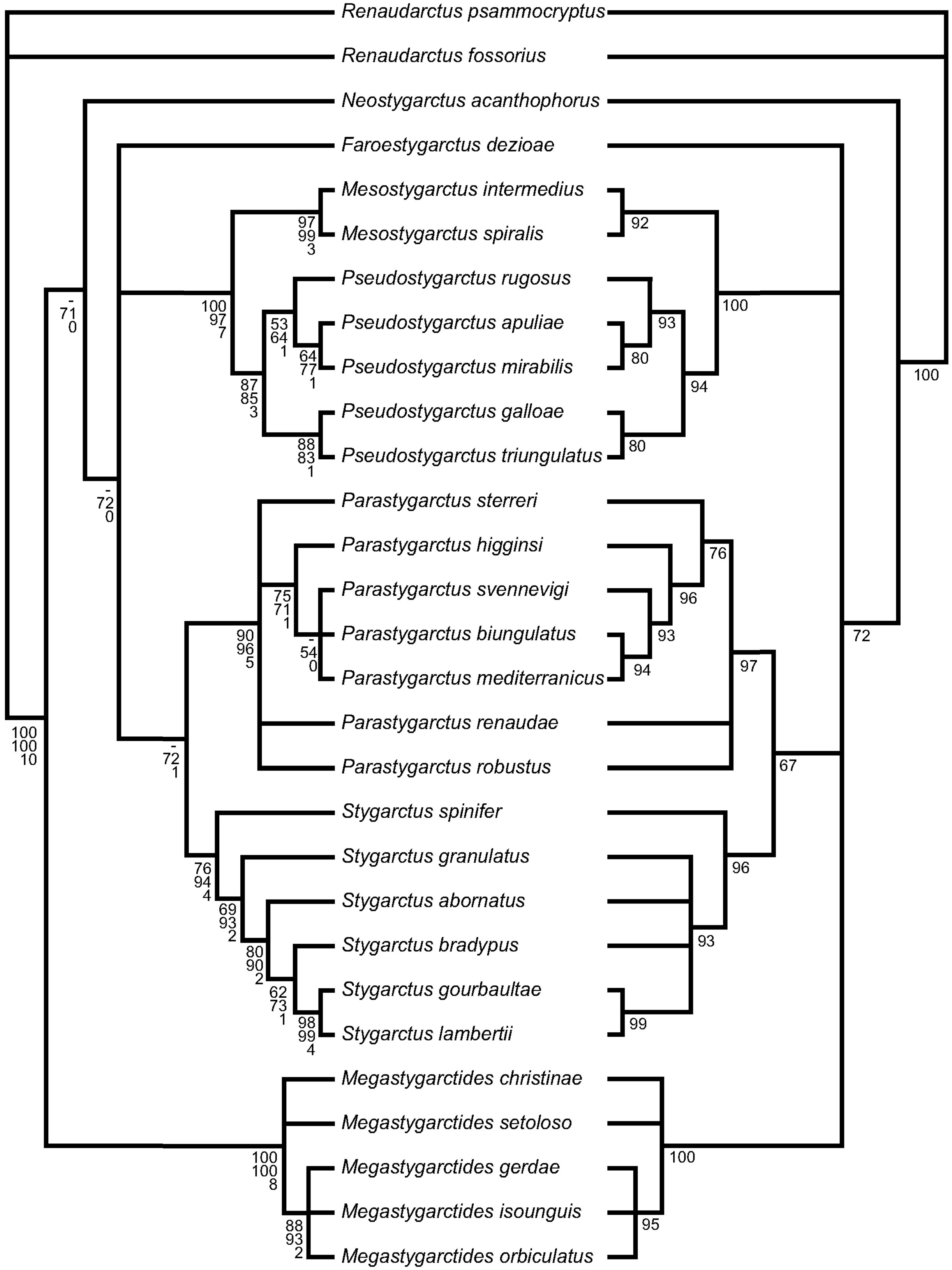

Renaudarctus psammocryptus
Renaudarctus fossorius
Neostygarctus acanthophorus
Faroestygarctus dezioae
Mesostygarctus intermedius
Mesostygarctus spiralis
Pseudostygarctus rugosus
Pseudostygarctus apuliae
Pseudostygarctus mirabilis
Pseudostygarctus galloae
Pseudostygarctus triungulatus
Parastygarctus sterreri
Parastygarctus higginsi
Parastygarctus svennevigi
Parastygarctus biungulatus
Parastygarctus mediterranicus
Parastygarctus renaudae
Parastygarctus robustus
Stygarctus spinifer
Stygarctus granulatus
Stygarctus abornatus
Stygarctus bradypus
Stygarctus gourbaultae
Stygarctus lambertii
Megastygarctides christinae
Megastygarctides setoloso
Megastygarctides gerdae
Megastygarctides isounguis
Megastygarctides orbiculatus
97 99 3
100 97 7
53 64 1
64 77 1
87 85 3
88 83 1
- 71 0
- 72 0
75 71 1
- 54 0
90 96 5
100 100 10
- 72 1
76 94 4
69 93 2
80 90 2
62 73 1
98 99 4
100 100 8
88 93 2
92
100
93
80
94
80
100
76
96
93
94
97
72
67
96
93
99
100
95

Table 9. Summary of the characters. The number of states, steps on the tree, consistency index (CI), retention index (RI) and rescaled consistency index (RC) for each character.

Character	States	Steps	CI	RI	RC	Character	States	Steps	CI	RI	RC
1	2	1	1.00	1.00	1.00	**42**	3	4	0.50	0.71	0.36
2	3	3	0.67	0.80	0.53	**43**	3	3	0.67	0.50	0.33
3	5	4	1.00	1.00	1.00	**44**	6	8	0.63	0.79	0.49
4	5	5	0.80	0.94	0.76	**45**	3	5	0.40	0.75	0.30
5	3	3	0.67	0.92	0.61	**46**	2	1	1.00	1.00	1.00
6	2	1	1.00	1.00	1.00	**47**	3	3	0.67	0.83	0.56
7	2	2	0.50	0.67	0.33	48	4	5	0.60	0.78	0.47
8	2	2	0.50	0.67	0.33	**49**	2	1	1.00	1.00	1.00
9	5	4	1.00	1.00	1.00	**50**	2	1	1.00	1.00	1.00
10	2	3	0.33	0.71	0.24	**51**	2	1	1.00	1.00	1.00
11	2	1	1.00	1.00	1.00	**52**	2	2	0.50	0.88	0.44
12	2	1	1.00	1.00	1.00	**53**	4	6	0.50	0.57	0.29
13	4	4	0.75	0.0	0.0	**54**	3	3	0.67	0.83	0.56
14	3	2	1.00	1.00	1.00	**55**	2	2	0.50	0.93	0.46
15	3	3	0.67	0.0	0.0	**56**	2	3	0.33	0.75	0.25
16	3	3	0.67	0.75	0.50	**57**	4	3	1.00	1.00	1.00
17	3	4	0.50	0.60	0.30	**58**	3	3	0.67	0.50	0.33
18	3	2	1.00	1.00	1.00	**59**	6	9	0.56	0.64	0.35
19	6	6	0.83	0.67	0.56	**60**	5	5	0.80	0.93	0.74
20	4	6	0.50	0.77	0.38	**61**	2	3	0.33	0.83	0.28
21	4	7	0.43	0.71	0.31	**62**	2	1	1.00	1.00	1.00
22	3	3	0.67	0.80	0.53	**63**	2	1	1.00	1.00	1.00
23	3	3	0.67	0.67	0.44	**64**	2	3	0.33	0.60	0.20
24	3	3	0.67	0.67	0.44	**65**	3	3	0.67	0.0	0.0
25	3	5	0.40	0.67	0.27	**66**	2	1	1.00	1.00	1.00

Character	States	Steps	CI	RI	RC	Character	States	Steps	CI	RI	RC
26	3	5	0.40	0.70	0.28	**67**	2	2	0.50	0.89	0.44
27	2	1	1.00	1.00	1.00	**68**	3	2	1.00	1.00	1.00
28	3	3	0.67	0.75	0.50	**69**	2	1	1.00	1.00	1.00
29	3	4	0.50	0.80	0.40	**70**	2	1	1.00	1.00	1.00
30	7	6	1.00	1.00	1.00	**71**	2	1	1.00	1.00	1.00
31	3	2	1.00	1.00	1.00	**72**	2	1	1.00	1.00	1.00
32	3	2	1.00	1.00	1.00	**73**	2	1	1.00	1.00	1.00
33	4	3	1.00	1.00	1.00	**74**	4	4	0.75	0.90	0.67
34	4	6	0.50	0.73	0.36	**75**	4	5	0.60	0.88	0.53
35	4	5	0.60	0.85	0.51	**76**	2	1	1.00	1.00	1.00
36	3	3	0.67	0.91	0.61	**77**	5	8	0.50	0.60	0.30
37	4	3	1.00	1.00	1.00	**78**	3	9	0.22	0.42	0.09
38	3	2	1.00	1.00	1.00	**79**	3	3	0.67	0.83	0.56
39	3	2	1.00	1.00	1.00	**80**	4	4	0.75	0.75	0.56
40	3	6	0.33	0.64	0.21	**81**	2	1	1.00	1.00	1.00
41	3	2	1.00	1.00	1.00						

Neoarctus. These were 1) the position of *Faroestygarctus* which varied from sister-group to (*Neostygarctus* + the remaining Stygarctinae) to an unresolved relationship with (*Mesostygarctus* + *Pseudostygarctus*) and (*Parastygarctus* + *Stygarctus*), and 2) the regular inference of the clade (*Parastygarctus* + *Stygarctus*), which was poorly supported to unsupported by the bootstrap analyses. *Parastygarctus* was the only genus where internal topological changes were inferred when *Renaudarctus* was used as the single outgroup or when either *Neostygarctus* or *Faroestygarctus* were removed from the analyses. The basal species (*P. robustus* or *P. renaudae*) shifted position or the basal relationships were unresolved. The cladograms with *Renaudarctus* spp. as the only outgroups are presented in figure 34.

The effect of removing *Coronarctus* and *Neoarctus* was much greater in the BI analyses, where the traditionally recognized Stygarctidae was inferred to be monophyletic with *Neostygarctus* as sister-group (Figure 34). The sister-group relationship between *Parastygarctus* and *Stygarctus* was also inferred, although weakly supported, by the BI analysis following the removal of *Coronarctus* and *Neoarctus*.

Kishino-Hasegawa tests: The Kishino-Hasegawa tests showed a non-significant difference between the most parsimonious tree and a tree topology where *Stygarctus spinifer* was the sister-group to of *Parastygarctus* ($P = 0.0514$). Significant differences were found between the most parsimonious tree and the *Mesostygarctus* clade as an unresolved basal part of *Pseudostygarctus* (P = 0.0416), and the most parsimonious tree and a monophyletic traditional Stygarctidae (Stygarctinae + Megastygarctidinae) with *Neostygarctus* as the sister-group (also P = 0.0416). Although the results from the KH-tests should be treated carefully the latter result suggests that Neostygarctidae is an artificial category and indicate support of the inclusion of this taxon in Stygarctinae.

Character tracing of different character systems

The consistency index (CI) values, which measures the amount of homoplasy, indicate that the legs and claws (average CI = 59.57) and the pharyngeal apparatus (average CI = 55.25) are much more homoplasious character systems than head lobes (average CI = 79.33), plates (average CI = 73.75), seminal receptacles (average CI = 78.75) and sense organs (average CI = 79.16) (Table 9).

Head lobes

A head differentiated into lobes (1) is a synapomorphy for Stygarctidae (including *Neostygarctus*). The number of head lobes (2) increases within Stygarctidae from three (*Megastygarctides* and *Faroestygarctus*) to five (the remaining genera including *Neostygarctus*). Within Stygarctinae the lobes get progressively more protruded (3) and within Stygarctinae the incision between the internal and external cirri becomes progressively deeper (4).

Segmental plates

Megastygarctides exhibits great variation in the intersegmental dorsal plates, from secondarily reduced plates to four and five plates (19). Four intersegmental dorsal plates is the most common number (generally there is no trend or progressive development of the segmental plates or plate sheets throughout the Stygarctidae). Intersegmental ridges (22) are lost in Stygarctinae (including *Neostygarctus*). The lateral processes of the body plates (30) develop from a simple single process into a single funnel-shaped process to two processes of varying shape. *Megastygarctides* has lost the lateral processes.

Seminal receptacles

The seminal receptacles (44-51) show remarkable variation within Stygarctidae, while at the same time being fairly conserved within the genera. Generally there is no trend or progressive development of the seminal receptacles throughout the Stygarctidae.

Legs and claws

Highly telescopic legs have evolved within Stygarctinae (except *Faroestygarctus dezioae*) and *Megastygarctides christinae* (52). The various claw characters (53-58) show no clear developmental series in Stygarctidae with much convergent evolution and ambiguity in the character state of the outgroups *Coronarctus* and *Neoarctus*. However, some character states are autapomorphic for specific groups.

Sense organs

The shape of the secondary clavae (60) evolved from globular to elongate club-shaped. Within Stygarctidae the primary and secondary clavae (61) evolves from being of similar shape to dissimilar in shape. The elongate, club-shaped secondary clavae becomes bent along the frontal lobe within *Stygarctus* (62). Within Stygarctinae (including *Neostygarctus*) the relative position of the primary clava and the external cirrus shifts, with the clava moving from the ventral to posterior position with respect to the cirrus (68). Within Stygarctidae the cirrus E evolves a process of varying size and position (75).

Examples of convergent evolution

Reference to the character and character state is given using the following notation (1:0), i.e. character 1, character state 0.

Convergent characters of the head lobes and sheets

The character state of three head lobes (2:2) which is the condition in *Faroestygarctus dezioae* and *Megastygarctides* spp. reappear in *Pseudostygarctus rugosus*. The presence of a ventral funnel-shaped cuticular structure between the internal and external cirri (4:4) is a convergence between *Pseudostygarctus rugosus* (male) and *Faroestygarctus dezioae* (female and paedomorphic). The frontal sheet of the head (7:0) and the sheet covering the indentation of the lateral lobe anterior to the lateral cirrus and primary clava (8:0) are both lost in *Pseudostygarctus apuliae*. The presence of these sheets is synapomorphic for *Pseudostygarctus* having originated in a *Pseudostygarctus* common ancestor but is absent in all the other species in the analysis.

Convergent characters of the segmental plates

Pillars in the cuticle have been convergently lost (10:0) in *Megastygarctides* spp. and *Mesostygarctus* spp. The presence of only segmental plates (13:1) and the absence of intersegmental plates (15:0) are convergences between *Neoarctus primigenius* and *Neostygarctus acanthophorus*. The presence of intersegmental plate ipI (16:1) is a convergence between *Pseudostygarctus apuliae* and *Megastygarctides* (all dorsal plates are secondarily reduced in *Megastygarctides gerdae*). The presence of intersegmental plate ipIV (17:1) is a convergence between *Parastygarctus biungulatus*, *Pseudostygarctus apuliae* and *Megastygarctides* (all dorsal plates are secondarily reduced in *Megastygarctides gerdae*). The presence of four intersegmental dorsal plates (19:3) is convergently evolved in *Pseudostygarctus apuliae* and *Megastygarctides isounguis*, *M. orbiculatus* and *M. setoloso*. The plesiomorphic character state of the intersegmental plates is unclear within Stygarctinae. An undivided sculpture of second intersegmental plate (ipII) (20:1) is present in the basal *P. renaudae* and *P. robustus*, *Stygarctus granulatus* and the clade (*Mesostygarctus*, *Pseudostygarctus*) and reappears in *Parastygarctus biungulatus*. Though the character tracing is equivocal for most of the relationships between the Stygarctidae genera. The sculpture of the third intersegmental plate (ipIII) (21) shows many convergent developments. The sculpture is absent (21:0) in most species of *Parastygarctus*, *Faroestygarctus dezioae* and *Megastygarctides*. A sculpture with median narrowing (21:1) is convergently present in most species of *Stygarctus* and *Renaudarctus*. A sculpture without median narrowing (21:2) is present in the basal *P. renaudae* and *P. robustus*, *Neostygarctus acanthophorus*, *Stygarctus granulatus* and the clade (*Mesostygarctus*, *Pseudostygarctus*) and reappears in *Parastygarctus biungulatus*. Dorsal spikes on the second body plate (23:1) and a longitudinal sculpture on body plates (24:1) have convergently evolved in the clade (*Stygarctus bradypus* (*S. gourbaultae*, *S. lambertii*)) and *S. spinifer*. A large ventral cephalic plate following the shape of the head (25:2) has convergently evolved in *Stygarctus* and *Mesostygarctus*. Ventral body plates (26:1) have convergently evolved in *Parastygarctus renaudae*, *Stygarctus*, the clade (*Mesostygarctus*, *Pseudostygarctus*) and *Renaudarctus*. Two lateral body plate processes (29:1) have convergently evolved in the clade (*Parastygarctus higginsi*, (*P. svennevigi*, (*P. biungulatus*, *P. mediterranicus*))), (*Stygarctus gourbaultae*, *S. lambertii*) and (*Mesostygarctus*, *Pseudostygarctus*). Anterior process, or anterior part of funnel-shaped process, of the body plates with a single-pointed termination (34:1) has convergently evolved in the clades (*Parastygarctus higginsi*, (*P. svennevigi*, (*P. biungulatus*, *P. mediterranicus*))), *Stygarctus* [except *S. spinifer*], *Mesostygarctus intermedius* and *Pseudostygarctus rugosus*. Body plates with agradually tapering short process (35:0) have convergently evolved in *Stygarctus* [except *S. spinifer*] and *Mesostygarctus* and, though the character tracing is equivocal, in *Renaudarctus*. Lateral body plate sheets (36:1) have convergently evolved in *Stygarctus* [except *S. spinifer*] and the clade (*Mesostygarctus*, *Pseudostygarctus*). Two pairs of lateral processes of the caudal plate (40:1) have convergently evolved in the clade (*P. svennevigi*, (*P. biungulatus*, *P. mediterranicus*)), *Stygarctus* [except *S. granulatus*], the clade (*Pseudostygarctus galloae*, *P. triungulatus*) and *Renaudarctus*. Caudal spikes (42:1) have convergently evolved in *Parastygarctus biungulatus*, *Stygarctus* [except *S. spinifer*] and *Renaudarctus*.

Convergent characters of the seminal receptacles

Seminal receptacle vesicle as a small enlargement of the terminal end (44:0) has convergently evolved in *Parastygarctus biungulatus* and the *Stygarctus* clade. A round vesicle, approximately the same size as the gonopore (44:3) has convergently evolved in *Neostygarctus acanthophorus* and *Renaudarctus*. A ventro-lateral vesicle of the seminal receptacle (45:0) has convergently evolved in *Stygarctus* [except *S. spinifer*], *Faroestygarctus dezioae*, *Renaudarctus* and *Neoarctus primigenius*. A seminal receptacle duct opening that overlaps the gonopore (47:0) has convergently evolved in the clade (*Mesostyg-*

arctus, *Pseudostygarctus*) and *Megastygarctides gerdae* and *M. orbiculatus*. Absence of the loop of the duct (48:0) is considered the plesiomorphic condition as it is absent in *Parastygarctus* [except *P. robustus*], *Faroestygarctus dezioae*, *Megastygarctides*, *Renaudarctus*, *Neoarctus primigenius* and *Coronarctus*.

Convergent characters of the legs and claws

Highly telescopic legs (52:1) have convergently evolved in *Megastygarctides christinae* and the large unresolved clade ((*Mesostygarctus*, *Pseudostygarctus*), *Neostygarctus*, (*Parastygarctus*, *Stygarctus*)). Two claws on all legs (53:1) have convergently evolved in *Parastygarctus biungulatus*, *Pseudostygarctus galloae* and *Faroestygarctus dezioae*, which represent paedomorphic species. Claws inserting via toes on foot (54:2) has convergently evolved in *Neostygarctus acanthophorus* and *Renaudarctus*. A thin long filament dorsal on the median claws (55:1) has convergently evolved in the clade (*Parastygarctus*, *Stygarctus*) and *Renaudarctus*. Claw accessories on all claws (56:1) have convergently evolved in *Pseudostygarctus triungulatus*, *Megastygarctides* and *Renaudarctus*. Claws consisting of a strongly cuticularized portion and a thin, more translucent laminar portion (58:2) have convergently evolved in *Neostygarctus acanthophorus* and *Renaudarctus*.

Convergent characters of the sense organs

Pedunculate, moderately elongate club-shaped primary clavae (59:1) has convergently evolved in the clade (*Parastygarctus biungulatus*, *P. mediterranicus*), *Stygarctus* [except *S. lamberti*], the clade (*Pseudostygarctus rugosus*, *P. apuliae*, *P. mirabilis*) and *Megastygarctides*. "Flattened" sausage-shaped secondary clavae (60:2) have convergently evolved in *Megastygarctides christinae* and *Renaudarctus*. Dissimilar primary and secondary clavae (61:1) have convergently evolved in *Stygarctus lambertii* and the clade (*Mesostygarctus*, *Pseudostygarctus*), *Faroestygarctus dezioae*, *Megastygarctides*, *Renaudarctus* and *Coronarctus verrucatus*, as the clavae are similar in the rest of the clade (*Parastygarctus*, *Stygarctus*) and *Neoarctus primigenius*. Median cirrus anterior on cephalic plate, not posterior to the incision between internal and external cirri (64:1) has convergently evolved in *Neostygarctus acanthophorus*, the clade (*Pseudostygarctus rugosus*, *P. apuliae*, *P. mirabilis*) and *Renaudarctus*. Internal cirri slightly ventral on the head (65:1) has convergently evolved in *Neostygarctus acanthophorus* and *Neoarctus primigenius*. External cirri frontal on the head (67:0) have convergently evolved in *Neostygarctus acanthophorus*, *Parastygarctus* and *Renaudarctus*. Cirrus E accordion articulation + flagellum (74:1) has convergently evolved in the clade (*Parastygarctus svennevigi*, (*P. biungulatus*, *P. mediterranicus*)), *Stygarctus*, *Megastygarctides*, *Renaudarctus*, *Neoarctus* and *Coronarctus*. Cirrus E not inserted on a process (75:0) has convergently evolved in *Parastygarctus biungulatus*, *Faroestygarctus dezioae* (both of which are paedomorphic), *Renaudarctus*, *Neoarctus* and *Coronarctus*. A pedunculate papilla with rounded termination on the fourth leg (77:1) has convergently evolved in *Parastygarctus*, the clades (*Stygarctus abornatus*, (*S. bradypus*, (*S. gourbaultae*, *S. lambertii*))) [though absent in *S. lambertii*], and (*Mesostygarctus*, *Pseudostygarctus*) [except *P. mirabilis*] and *Megastygarctides gerdae*.

Convergent characters of the mouth and buccal apparatus

The plesiomorphic character state of the position of the mouth is unclear within Stygarctinae. A terminal mouth (78:0) has convergently evolved in *Parastygarctus higginsi*, *P. svennevigi*, *Stygarctus granulatus* and *Coronarctus*. A ventral mouth (78:2) has convergently evolved in *Neostygarctus acanthophorus*, the clade (*Stygarctus bradypus*, (*S. gourbaultae*, *S. lambertii*)), *Pseudostygarctus* [except *P. mirabilis*] and *Renaudarctus*.

Placoids without internal stylet support (79:1) have convergently evolved in *Neostygarctus acanthophorus*, *Megastygarctides*, *Renaudarctus* and *Neoarctus primigenius*. Bifurcate stylet furcae pointing posteriorly (80:1) has convergently evolved in *Neostygarctus acanthophorus* and *Renaudarctus*.

Convergent characters between Neostygarctus and more basal taxa

Neostygarctus has evolved seven characters which are also present in *Renaudarctus* but not in the branch leading towards *Neostygarctus*. They are currently interpreted as homoplasies (convergences), but might imply that the phylogenetic position of *Neostygarctus* should be closer to *Renaudarctus* than inferred by the present analyses. The characters are: 44(2) the seminal receptacles have round vesicles, 54(2) the claws insert on the foot via toes, 58(2) the claws are not j-shaped, consisting of a strongly cuticularized portion and a thin, more translucent laminar portion, 64(1) the median cirrus is placed anteriorly on the cephalic plate (also present in the Mediterranean clade of *Pseudostygarctus*), 78(2) the mouth opening is ventral (also evolved within species of *Pseudostygarctus* and *Stygarctus*), 79(1) the placoids without internal stylet support (also evolved in *Megastygarctides* and *Neoarctus*), 80(1) the bifurcate stylet furcae point posteriorly.

Furthermore *Neostygarctus* share two characters with *Neoarctus* also perhaps implying a more basal position of *Neostygarctus* than inferred by the present analyses (except BI analysis with *Renaudarctus* as the only outgroup). The two characters are: 13(1) only segmental plates present, and 65(1) internal cirri slightly ventral on the head.

Discussion

Although we have thoroughly analyzed a comprehensive data matrix, much uncertainty still exists regarding the phylogenetic relationships of the different stygarctid genera. The uncertainties are due to low branch support (bootstrap, Bremer support and posterior probability values) and unresolved nodes resulting from homoplasy in the data.

The impact of the phylogenetic analyses on the classification of the Stygarctidae depends partly on the selected outgroups. The results from most analyses indicate that Stygarctidae, as currently defined, is paraphyletic because Neostygarctidae is included within the clade. We have decided to keep the current family status of the Stygarctidae, which then will include the two subfamilies Megastygarctidinae and Stygarctinae (now including *Neostygarctus*) (Table 10).

Table 10. The proposed classification of the Stygarctidae.

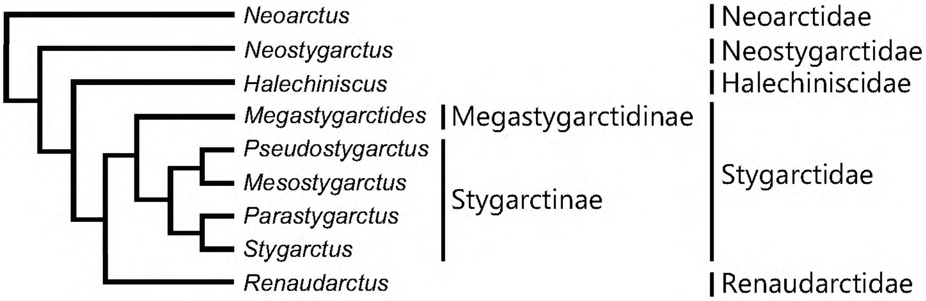
Family Stygarctidae		
	Subfamily Stygarctinae	
		Genus *Faroestygarctus*
		Genus *Mesostygarctus*
		Genus *Neostygarctus*
		Genus *Parastygarctus*
		Genus *Pseudostygarctus*
		Genus *Stygarctus*
	Subfamily Megastygarctidinae	
		Genus *Megastygarctides*

This solution removes the family status of Neostygarctidae, but it does not require family or subfamily status of *Faroestygarctus* or any of the other clades in Stygarctinae. Two other solutions are also possible but are not equally justifiable: 1) the family Stygarctidae could include the four subfamilies Megastygarctidinae, Neostygarctinae, Stygarctinae and "Faroestygarctinae", or 2) to elevate Megastygarctidinae, Stygarctinae and *Faroestygarctus* to family level so the clade includes the four families "Megastygarctididae", Neostygarctidae, Stygarctidae and "Faroestygarctidae". These two solutions would require the erection of a new monotypic family constituted of *Faroestygarctus*, due to the inferred phylogenetic position resulting from the analyses based on the complete data matrix. However, the traditional Stygarctinae, including the genera *Mesostygarctus*, *Parastygarctus*, *Pseudostygarctus*, and *Stygarctus*, does not form a monophyletic group in our analyses. Only the BI analysis with *Renaudarctus* as the only outgroup does not infer a paraphyletic Stygarctidae, though, the posterior probability only weakly supports a monophyletic Stygarctidae. The Kishino-Hasegawa test showed that a classification with *Neostygarctus* within Stygarctidae was significantly better than a classification with distinct Neostygarctidae and Stygarctidae.

Our analyses indicate that all the currently recognized genera are monophyletic, the generic status of *Mesostygarctus* is strongly supported by the sister-group relationship with *Pseudostygarctus* inferred by both MP and BI analyses. The assignment of *Mesostygarctus intermedius* to *Pseudostygarctus*, as proposed by Gallo D'Addabbo et al. (2001), would only have been justified if our analyses showed that *M. intermedius* was placed within the *Pseudostygarctus* species and not basal to them. The KH-test also showed that a monophyletic *Pseudostygarctus* was significantly better than a tree with an unresolved relationship between the two major evolutionary *Pseudostygarctus* lineages and *Mesostygarctus*. With the additional *M. spiralis* nov. sp. description we further emphasize the validity of the genus and reinstate *Mesostygarctus*.

Based on the development of the lateral processes in the genus *Pseudostygarctus* Gallo D'Addabbo et al.

Figure 35. The phylogeny of Stygarctidae and some related genera as proposed by Bello & Grimaldi de Zio (1998).



(2000) stated that *P. mirabilis* was the most evolved and *P. triungulatus* the most primitive. For this statement to be supported by cladogram topology the *Pseudostygarctus* tree would have to be stepped with *P. mirabilis* at the top and *P. triungulatus* at the bottom. Our results provide little support of this view, as *Pseudostygarctus* is divided into two major clades or lineages - a Mediterranean and a "neotenic" clade (Figure 32). *Pseudostygarctus mirabilis* is the sister-group to *P. apuliae* in the Mediterranean clade which has *P. rugosus* at its base. *Pseudostygarctus triungulatus* shares a sister-group relationship with *P. galloae* in the neotenic clade. However, it only takes a single step to place *P. triungulatus* basal in the tree.

The phylogenetic position of the neotenic species within *Parastygarctus* and *Pseudostygarctus* indicates that neotenic species are not necessarily close to the basal node of their respective generic clades. *Parastygarctus biungulatus* was placed, by most analyses, as the most evolved taxon in the *Parastygarctus* clade (forming a clade with *P. mediterranicus*). As discussed above *Pseudostygarctus triungulatus* and *P. galloae* were placed in the "neotenic" lineage in the *Pseudostygarctus* clade.

The current classification of the enigmatic *Stygarctus spinifer* was justified according to our results, although the KH-test did not show a significant relationship to *Stygarctus*. In all our analyses *S. spinifer* was inferred to be the basal member of *Stygarctus* and we therefore cannot support the view by Gallo D'Addabbo et al. (2001) that it should be transferred to *Parastygarctus*.

Bello & Grimaldi de Zio (1998) inferred a sister-group relationship between *Stygarctus* and *Parastygarctus* (Figure 35), which we support.

However, our results from the different analyses were partly incongruent as the unweighted MP and the BI analyses of the complete data matrix showed an unresolved polytomy of (*Neostygarctus*, (*Mesostygarctus* + *Pseudostygarctus*), *Parastygarctus*, *Stygarctus*). Still, the clade is supported by seven character states and we regard it as the most probable topology.

The data matrix has a high number of convergent character states represented by both loss and development of character states absent or present in other parts of the cladogram. The convergent character states are present in all the character systems. These convergent characters can be regarded as evolution towards a better suited morphology for a specific environment, erroneous character state designation or an implication that the inferred phylogeny is just the best current working hypothesis until more taxa and characters are included in the analyses.

Conclusions

The most significant results from the phylogenetic analyses are 1) the inclusion of the Neostygarctidae within the Stygarctidae; 2) the distant relationship between the Stygarctinae and the Megastygarctidinae; 3) the basal position of the new genus *Faroestygarctus* within the Stygarctinae. Based on our phylogenetic results we recommend the inclusion of *Neostygarctus acanthophorus* in Stygarctinae. The proposed classification is presented in Table 10.

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Appendix 1:

List of characters and character states

1 Head region subdivision: 0 head lobes absent; 1 head differentiated in lobes

2 Number of head lobes: 0 five lobes; 1 four lobes; 2 three lobes

3 Protrusion of head lobes: 0 all lobes moderately protruded to about the same extent; 1 all lobes greatly protruded to about the same extent; 2 lateral lobes greatly protruded; 3 lateral lobes moderately protruded; 4 anterior lobes more protruded than lateral lobes

4 Anterior part of the head: 0 incision absent between internal and external cirri; 1 moderate incision between internal and external cirri; 2 deep incision between internal and external cirri; 3 deep incision with a thin membrane; 4 ventral funnel-shaped cuticular structure between the internal and external cirri

5 Lateral lobe of the head with posterior spine: 0 posterior spine absent; 1 posterior spine present

6 Lateral lobe of the head with posterior sheet: 0 sheet absent; 1 sheet present

7 Frontal sheet of head: 0 absent; 1 present

8 Sheet covering indentation of the lateral lobe anterior to the lateral cirrus and primary clava: 0 absent; 1 present

9 Shape of the head: 0 almost semi-circular; 1 with large "neck" extension; 2 extended anteriorly-posteriorly; 3 compact head inserted directly on the body; 4 head not fused with scapular plate

10 Pillars in the cuticle: 0 absent; 1 present. (These observations are based on light microscopy technique only)

11 Outline of body cross section: 0 round; 1 dorso-ventral flattened

12 Dorsal leg plate: 0 absent; 1 present (*Renaudarctus*)

13 Cuticular body plates: 0 absent (*Coronarctus*); 1 only segmental plates present; 2 segmental and intersegmental plates present; 3 segmental and intersegmental plates secondarily reduced. (In the following plate characters *Coronarctus verrucatus* has been scored as inapplicable due to the absence of plates, whereas *Megastygarctides gerdae* has been scored as segmental and intersegmental plates secondarily reduced)

14 Relative thickness of the dorsal body plates and the intersegmental plates: 0 body plates thicker than intersegmental plates; 1 body plates and intersegmental plates of equal thickness; 2 dorsal body plates secondarily reduced

15 Intersegmental plates: 0 absent; 1 present; 2 intersegmental plates secondarily reduced

16 Intersegmental plate ipI: 0 absent; 1 present; 2 intersegmental dorsal plate secondarily reduced

17 Intersegmental plate ipIV: 0 absent; 1 present; 2 intersegmental dorsal plate secondarily reduced

18 Size of intersegmental dorsal plates: 0 intersegmental dorsal plates small; 1 intersegmental dorsal plates large; 2 intersegmental dorsal plates secondarily reduced

19 Number of intersegmental dorsal plates: 0 one plate; 1 two plates; 2 three plates; 3 four plates; 4 five plates; 5 intersegmental dorsal plates secondarily reduced. (In *Megastygarctides christinae* there are two intersegmental plates between the cephalic plate and the first body plate, resulting in a total of five intersegmental plates)

20 Sculpture of second intersegmental plate (ipII): 0 sculpture absent; 1 sculpture undivided; 2 sculpture divided; 3 intersegmental dorsal plate secondarily reduced

21 Sculpture of third intersegmental plate (ipIII): 0 sculpture absent; 1 sculpture with median narrowing; 2 sculpture without median narrowing; 3 intersegmental dorsal plate secondarily reduced

22 Intersegmental ridges: 0 absent; 1 present; 2 intersegmental ridges secondarily reduced

23 Dorsal spikes on the second body plate: 0 dorsal spikes absent; 1 dorsal spikes present; 2 dorsal plates secondarily reduced

24 Longitudinal sculpture on body plates: 0 longitudinal sculpture absent; 1 longitudinal sculpture present; 2 dorsal plates secondarily reduced

25 Ventral cephalic plate: 0 absent; 1 large plate not following the shape of the head; 2 large plate following the shape of the head

26 Ventral body plates: 0 absent; 1 plates present; 2 plates continues with dorsal plates

27 Ventral segmental cuticular folds: 0 absent; 1 present (*Mesostygarctus*)

28 Lateral processes of the body plates: 0 lateral processes absent; 1 lateral processes present; 2 dorsal plates secondarily reduced

29 Number of lateral processes of the body plates: 0 one process, 1 two processes; 2 dorsal plates secondarily reduced

30 Shape of the lateral processes of the body plates: 0 one process, more or less funnel-shaped; 1 one process, not funnel-shaped; 2 two similar gradually tapering long processes; 3 two processes, one of which are more or less funnel-shaped; 4 two processes, one of which ends in a long flexible spine (*Pseudostygarctus*); 5 two similar posterior processes (*Mesostygarctus*); 6 dorsal plates secondarily reduced

31 Funnel-shaped lateral process: 0 funnel-shaped lateral process absent; 1 funnel-shaped lateral process present; 2 dorsal plates secondarily reduced

32 Spines of funnel-shaped lateral process: 0 without anterior spines; 1 with anterior spines; 2 dorsal plates secondarily reduced

33 Relative position of the two lateral processes: 0 arranged in the same level; 1 arranged antero-ventral and postero-dorsal; 2 two posterior processes arranged latero-ventral and latero-dorsal; 3 dorsal plates secondarily reduced

34 Anterior process, or anterior part of funnel-shaped process, of the body plates: 0 anterior process absent; 1 single-pointed termination; 2 not single-pointed termination; 3 dorsal plates secondarily reduced

35 Posterior process/processes of the body plates: 0 gradually tapering short process; 1 less gradually tapering long process; 2 ending in long flexible spine; 3 dorsal plates secondarily reduced

36 Lateral sheets of the body plates: 0 sheets absent; 1 sheets present; 2 dorsal plates secondarily reduced

37 Lateral sheets of the body plates: 0 sheets present only terminally on the funnel-shaped ventro-lateral processes (*Stygarctus*); 1 sheets present along the margin of the lateral processes (*Pseudostygarctus*); 2 sheets present only on the dorso-lateral margin of the body plates (not associated with the ventro-lateral processes) (*Mesostygarctus*); 3 dorsal plates secondarily reduced

38 Size of the lateral sheets of the body plates: 0 small sheets; 1 large sheets; 2 dorsal plates secondarily reduced

39 Striation (ribs) of the lateral sheets of the body plates: 0 striation absent; 1 striation present; 2 dorsal plates secondarily reduced

40 Number of lateral processes of the caudal plate: 0 one pair of lateral processes; 1 two pairs of lateral processes; 2 dorsal plates secondarily reduced

41 Sheets of the lateral process of the caudal plate: 0 sheets absent; 1 sheets present; 2 dorsal plates secondarily reduced

42 Caudal spikes: 0 absent; 1 present; 2 dorsal plates secondarily reduced

43 Caudal spike sheets: 0 without sheets; 1 with sheets; 2 dorsal plates secondarily reduced

44 Vesicle of seminal receptacle: 0 small enlargement of the terminal end; 1 large elongate thickening; 2 round vesicle, approximately the same size as the gonopore; 3 round vesicle, larger than the gonopore; 4 large pouch; 5 large round spiral

45 Position of the seminal receptacle vesicle: 0 ventro-lateral; 1 ventral; 2 dorso-lateral

46 Opening of seminal receptacle duct: 0 close to the gonopore; 1 far away from the gonopore

47 When opening of seminal receptacle duct close to the gonopore: 0 overlapping the gonopore; 1 in close proximity to the gonopore; 2 genital spine

48 Loop of the duct: 0 absent; 1 close to the vesicle; 2 close to the duct opening; 3 intermediate between the vesicle and the duct opening

49 Cuticular bars at the opening of the seminal receptacle duct: 0 absent; 1 present

50 Cuticular pockets at the opening of the seminal receptacle duct: 0 absent; 1 present

51 Complex external genital cuticular structure: 0 absent; 1 present. (In *Megastygarctides*, the genital ducts of the two seminal receptacles are extended out of the body as two long and robust hollow spines, or as two small ovoid papillae)

52 Telescopic legs: 0 weakly telescopic; 1 highly telescopic

53 Number of claws per leg: 0 four on all legs; 1 two on all legs; 2 three on all legs; 3 four on the first three pairs of legs, two on the last pair

54 Claw insertion: 0 claws inserted directly on the leg; 1 claws originate from a short pedestal; 2 claws inserted on foot via toes

55 Median claws dorsal accessory structures: 0 bristle or spine; 1 thin long filament

56 Distribution of claw accessories (bristles, spines, long filaments): 0 only on medial claws; 1 on all claws. (In the original description by McKirdy et al. (1976) *Pseudostygarctus biungulatus* was stated to have spines on all three claws. Knowing that all other *Pseudostygarctus* species possess accessory spines only on medial claws, it is likely that the observation of McKirdy et al. (1976) is a misinterpretation. However, our re-examining of the type material of this species could not establish whether there is an accessory spine present on the third claw. Consequently, we have scored *Pseudostygarctus biungulatus* as having accessory spines on all claws)

57 Claw size: 0 claws on the first three pairs of legs of approximately the same size, claws on the fourth pair of legs slightly larger; 1 claws on the first three pairs of legs of approximately the same size, claws on the fourth pair of legs much larger; 2 claws of different size between each pairs of legs; 3 all claws of the same size

58 Claw shape: 0 claw j-shaped with well-developed basal spur; 1 claw j-shaped without basal spur; 2 claw not j-shaped, consisting of a strongly cuticularized portion and a thin, more translucent laminar portion

59 Shape of primary clavae: 0 pedunculate strongly elongate club-shaped; 1 pedunculate moderately elongate club-shaped; 2 pedunculate ovoid; 3 elongate with spine-like termination; 4 semi-globular; 5 ovoid with spine-like termination (*Neostygarctus*)

60 Shape of secondary clavae: 0 elongate, club-shaped; 1 semi-globular; 2 "flattened" sausage-shaped; 3 coronate; 4 globular

61 Primary and secondary clavae: 0 similar in shape; 1 not similar in shape

62 Elongate, club-shaped secondary clavae: 0 erect; 1 bent along the frontal lobe

63 Tertiary clavae: 0 absent; 1 present. (*Coronarctus*) has been scored as having tertiary clavae, as we believe the coronate sensory structure to be fused secondary and tertiary clavae)

64 Placement of median cirrus: 0 central on the head, posterior to incision between internal and external cirri; 1 anterior on cephalic plate, not posterior to the incision between internal and external cirri

65 Position of internal cirri: 0 frontal on the latero-frontal edge of the head; 1 slightly ventral on the head; 2 slightly dorsal (*Coronarctus*)

66 Insertion of internal cirri: 0 inserted on a distinct head lobe; 1 not inserted on a distinct head lobe

67 Position of external cirri: 0 frontal on the head; 1 ventral on the head

68 Relative position of primary clava and lateral cirrus: 0 clava posterior to cirrus; 1 clava ventral to cirrus; 2 clava dorsal to cirrus

69 Relative position of secondary clava and external cirrus: 0 secondary clava situated slightly anterior to the external cirrus or arising from approximately the same level; 1 secondary clava situated posterior to the external cirrus

70 Position of secondary clava and external cirrus: 0 not arising from ventral pedestal; 1 arising from ventral pedestal

71 Position of internal cirrus, external cirrus and secondary clava: 0 not on the same distinct head lobe; 1 on the same distinct head lobe

72 Deep incision between internal cirri: 0 absent; 1 present

73 Cirrus E insertion: 0 telescopically; 1 "ball and socket"

74 Cirrus E structure: 0 smooth proximal part + accordion articulation + flagellum; 1 accordion articulation + flagellum; 2 long tapering spine; 3 long and hair-like

75 Placement of cirrus E: 0 not inserted on a process; 1 on a dorso-lateral process; 2 on the end of large lateral process; 3 on a small ventro-lateral process

76 Distribution of sense organs on the legs: 0 on all four pairs of legs; 1 only on the fourth pair of legs. (In the original description by McKirdy et al. (1976) of *Megastygarctides orbiculatus* and *Stygarctus abornatus* the distribution of leg sense organs was stated to be on the last three pairs of legs and on all four pairs of legs, respectively. Our observations of the type material for these species only recognized sense organs on the fourth pair of legs. This was already reported for *M. orbiculatus* in Hansen & Kristensen (2006). Nearly all taxa in Halechiniscidae have sense organs on all four legs emphasising that the synapomorphy, leg sense organs only on the fourth pair of legs, of Renaudarctidae and the stygarctids is not an artefact of the chosen outgroups)

77 Sense organ on the fourth leg: 0 spherical papilla; 1 pedunculate papilla with rounded termination; 2 elongate papilla with pointed termination (*Neostygarctus*); 3 elongate papilla with terminal spine (*Neoarctus*); 4 spine-like cirrus (*Coronarctus*)

78 Position of mouth: 0 terminal; 1 sub-terminal; 2 ventral. (The mouth is considered terminal when it is positioned as in *Coronarctus* and ventral when it is positioned as in *Renaudarctus*. All other positions are considered sub-terminal)

79 Pharyngeal bulb: 0 placoids with internal stylet support; 1 placoids without internal stylet support; 2 placoids absent

80 Shape of the stylet furca: 0 double club-shaped stylet furcae; 1 bifurcate stylet furcae pointing posteriorly; 2 bifurcate stylet furcae bent anteriorly; 3 trifurcate stylet furcae with two large lateral lobes and a small terminal rod

81 Position of pharyngeal bulb in body: 0 pharyngeal bulb lying in first body segment; 1 pharyngeal bulb located behind the first body segment

Table 11. Character matrix.

	Head lobes/sheets									**Plate characters**																								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Outgroup taxa																																		
Coronarctus verrucatus	0	n	n	3	0	n	n	n	n	0	0	0	0	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Neoarctus primigenius	0	n	n	4	0	n	n	0	n	1	0	0	1	n	0	n	n	n	n	n	n	0	0	0	0	0	0	0	n	n	n	n	n	0
Neostygarctus acanthophorus	1	2	0	1	1	0	0	0	0	1	1	0	1	n	0	n	n	n	n	n	n	0	0	0	0	0	0	1	0	1	0	n	n	0
Renaudarctus psammocryptus	0	n	n	3	0	n	n	0	n	1	0	1	2	0	1	0	0	0	1	2	1	1	0	0	1	1	0	1	0	1	0	n	n	0
Renaudarctus fossorius n. sp.	0	n	n	3	0	n	n	0	n	1	0	1	2	0	1	0	0	0	1	2	1	1	0	0	1	1	0	1	0	1	0	n	n	0
Ingroup taxa																																		
Faroestygarctus dezioae n. sp.	1	0	2	1	4	0	0	0	0	1	1	0	2	0	1	0	0	0	0	n	0	0	0	0	0	0	0	1	0	1	0	n	n	0
Megastygarctides christinae	1	3	2	2	0	0	0	0	0	0	0	0	2	1	1	1	1	1	4	0	0	1	0	0	1	2	0	0	n	n	n	n	n	0
Megastygarctides gerdae	1	4	1	2	0	0	0	0	0	0	0	0	3	2	2	2	2	2	5	3	3	2	2	2	1	0	0	2	2	6	2	2	3	3
Megastygarctides isounguis	1	4	1	2	0	0	0	0	0	0	0	0	2	1	1	1	1	1	3	0	0	1	0	0	0	0	0	0	n	n	n	n	n	0
Megastygarctides orbiculatus	1	4	1	2	0	0	0	0	0	0	0	0	2	1	1	1	1	1	3	0	0	1	0	0	0	0	0	0	n	n	n	n	n	0
Megastygarctides setoloso	1	3	2	2	0	0	0	0	0	0	0	0	2	1	1	1	1	1	3	0	0	1	0	0	0	0	0	0	n	n	n	n	n	0
Mesostygarctus intermedius	1	0	0	1	3	0	0	0	0	0	1	0	2	0	1	0	0	0	1	1	2	0	0	0	2	?	1	1	1	5	0	n	?	1
Mesostygarctus spiralis n. sp.	1	0	0	1	3	0	0	0	0	0	1	0	2	0	1	0	0	0	1	1	2	0	0	0	2	1	1	1	1	5	0	n	2	0
Parastygarctus biungulatus	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	1	0	2	1	2	0	0	0	0	?	0	1	1	2	0	n	1	1
Parastygarctus higginsi	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	n	n	1
Parastygarctus mediterranicus	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	?	0	1	1	2	0	n	1	1
Parastygarctus renaudae	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	1	0	1	0	1	0	n	n	0
Parastygarctus sterreri	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	n	n	0
Parastygarctus svennevigi n. sp.	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	2	0	n	1	1
Parastygarctus robustus n. sp.	1	1	0	1	2	1	0	0	0	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	n	n	0
Pseudostygarctus apuliae	1	0	0	1	3	1	0	0	0	1	1	0	2	0	1	1	1	0	3	1	2	0	0	0	0	1	0	1	1	4	0	n	0	2
Pseudostygarctus galloae n. sp.	1	0	0	1	3	1	0	1	1	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	1	0	1	1	4	0	n	0	0
Pseudostygarctus mirabilis	1	0	0	1	3	1	0	1	1	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	1	0	1	1	4	0	n	0	2
Pseudostygarctus rugosus	1	0	2	1	4	0	0	1	1	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	?	0	1	1	4	0	n	0	1
Pseudostygarctus triungulatus	1	0	0	0	3	1	0	1	1	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	0	0	0	1	1	4	0	n	0	0
Stygarctus abornatus	1	0	0	0	1	1	1	0	0	1	1	0	2	0	1	0	0	0	1	2	1	0	0	0	?	?	0	1	0	0	1	0	n	1
Stygarctus bradypus	1	0	0	0	1	1	0	0	0	1	1	0	2	0	1	0	0	0	1	2	1	0	1	1	2	?	0	1	0	0	1	0	n	1
Stygarctus gourbaultae	1	0	0	0	1	1	1	0	0	1	1	0	2	0	1	0	0	0	1	2	1	0	1	1	2	1	0	1	1	3	1	1	0	1
Stygarctus granulatus	1	0	0	0	1	1	0	0	0	1	1	0	2	0	1	0	0	0	1	1	2	0	0	0	2	1	0	1	0	0	1	0	n	1
Stygarctus lambertii	1	0	0	0	1	1	1	0	0	1	1	0	2	0	1	0	0	0	1	2	1	0	1	1	2	1	0	1	1	3	1	1	0	1
Stygarctus spinifer	1	0	0	0	1	1	0	0	0	1	1	0	2	0	1	0	0	0	1	2	1	0	1	1	2	1	0	1	0	1	0	n	n	0

									Seminal Recep.								Legs/claws							Sense organs																			Pha. App.			
3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	8	8
5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
n	n	n	n	n	n	n	n	n	4	1	1	n	0	0	0	0	0	0	0	0	0	1	0	2	3	1	n	1	0	2	1	1	1	0	0	n	0	0	1	0	0	4	0	2	0	0
n	0	n	n	n	n	n	0	n	1	0	1	n	0	0	0	0	0	2	0	0	1	3	1	4	1	0	n	1	0	1	1	1	1	0	0	n	0	0	1	0	0	3	1	1	?	0
1	0	n	n	n	0	0	0	n	2	1	0	1	1	0	0	0	1	0	2	0	0	3	2	5	4	1	n	0	1	1	0	0	0	0	0	0	0	0	0	1	1	2	2	1	1	0
0	0	n	n	n	1	0	1	0	2	0	0	1	0	0	0	0	0	0	2	1	1	3	2	2	2	1	n	1	1	0	1	0	1	0	0	n	0	0	1	0	1	0	2	1	1	0
0	0	n	n	n	1	0	1	0	2	0	0	1	0	0	0	0	0	0	2	1	1	3	2	2	2	1	n	1	1	0	1	0	1	0	0	n	0	0	1	0	1	0	2	1	1	0
2	0	n	n	n	0	0	0	n	1	0	0	1	0	0	0	0	0	1	0	0	0	3	1	2	1	1	n	0	0	0	0	1	0	0	0	0	0	0	3	0	1	0	1	0	3	0
n	0	n	n	n	0	n	0	n	4	1	0	2	0	0	0	1	1	3	1	0	1	2	1	1	2	1	n	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	1	?	0
3	2	3	2	2	2	2	2	2	4	1	0	0	0	0	0	1	0	3	1	0	1	2	1	1	1	1	n	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	?	0
n	0	n	n	n	0	n	0	n	?	?	?	?	?	0	0	?	0	3	1	0	1	2	1	1	1	1	n	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	1	?	0
n	0	n	n	n	0	n	0	n	4	1	0	0	0	0	0	1	0	3	1	0	1	2	1	1	1	1	n	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	?	?	?
n	0	n	n	n	0	n	0	n	?	?	?	?	?	0	0	?	0	3	1	0	1	2	1	1	1	1	n	0	0	0	0	1	2	0	0	0	0	0	1	1	1	0	1	?	?	0
0	1	2	0	0	0	0	0	n	3	1	0	0	1	1	1	0	1	0	0	0	0	3	1	3	1	1	n	0	0	0	0	1	0	0	0	0	0	0	2	2	1	1	1	0	3	0
0	1	2	0	0	0	0	0	n	5	1	0	0	1	1	1	0	1	0	0	0	0	3	1	3	1	1	n	0	0	0	0	1	0	0	0	0	0	0	2	2	1	1	1	?	?	0
1	0	n	n	n	1	0	1	0	0	2	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	?	?	?
1	0	n	n	n	0	0	0	n	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	2	1
1	0	n	n	n	1	0	0	n	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	?	?	1
1	0	n	n	n	0	0	0	n	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	2	1
1	0	n	n	n	0	0	0	n	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	?	?	1
1	0	n	n	n	1	0	0	n	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	2	1
1	0	n	n	n	0	0	0	n	1	2	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	?	?	?
2	1	1	1	1	0	0	0	n	3	1	?	?	1	1	?	0	1	0	0	0	0	3	1	1	1	1	n	0	1	0	0	1	0	0	0	0	0	1	2	2	1	1	2	?	?	0
2	1	1	0	0	1	0	0	n	3	1	0	0	1	1	1	0	1	1	0	0	0	3	1	3	1	1	n	0	0	0	0	1	0	0	0	0	0	1	2	2	1	1	2	?	?	0
2	1	1	1	1	0	0	0	n	3	1	0	0	1	1	1	0	1	0	0	0	0	3	1	1	1	1	n	0	1	0	0	1	0	0	0	0	0	1	2	2	1	0	1	?	?	?
2	1	1	1	0	0	0	0	n	?	?	?	?	?	?	?	0	1	0	0	0	0	3	1	1	1	1	n	0	1	0	0	1	0	0	0	0	0	1	2	2	1	1	2	?	?	0
2	1	1	0	0	1	0	0	n	3	1	0	0	?	1	1	0	1	2	0	0	1	3	1	3	1	1	n	0	0	0	0	1	0	0	0	0	0	1	2	2	1	1	2	?	?	?
0	1	0	0	0	1	0	1	1	?	?	?	?	?	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	3	1	1	?	?	?	?
0	1	0	0	0	1	0	1	0	0	?	0	1	3	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	?	0	0	0	1	3	1	1	2	0	3	0
0	1	0	0	0	1	1	1	1	0	0	0	1	2	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	3	1	1	2	0	3	0
0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	3	1	0	0	0	?	0
0	1	0	0	0	1	1	1	1	0	0	0	1	2	0	0	0	1	0	0	1	0	0	1	2	0	1	1	0	0	0	0	1	0	0	1	0	0	0	1	3	1	0	2	?	?	?
1	0	n	n	n	1	0	0	n	0	1	0	1	2	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	3	1	0	1	?	?	0