UNIVERSITEIT GENT

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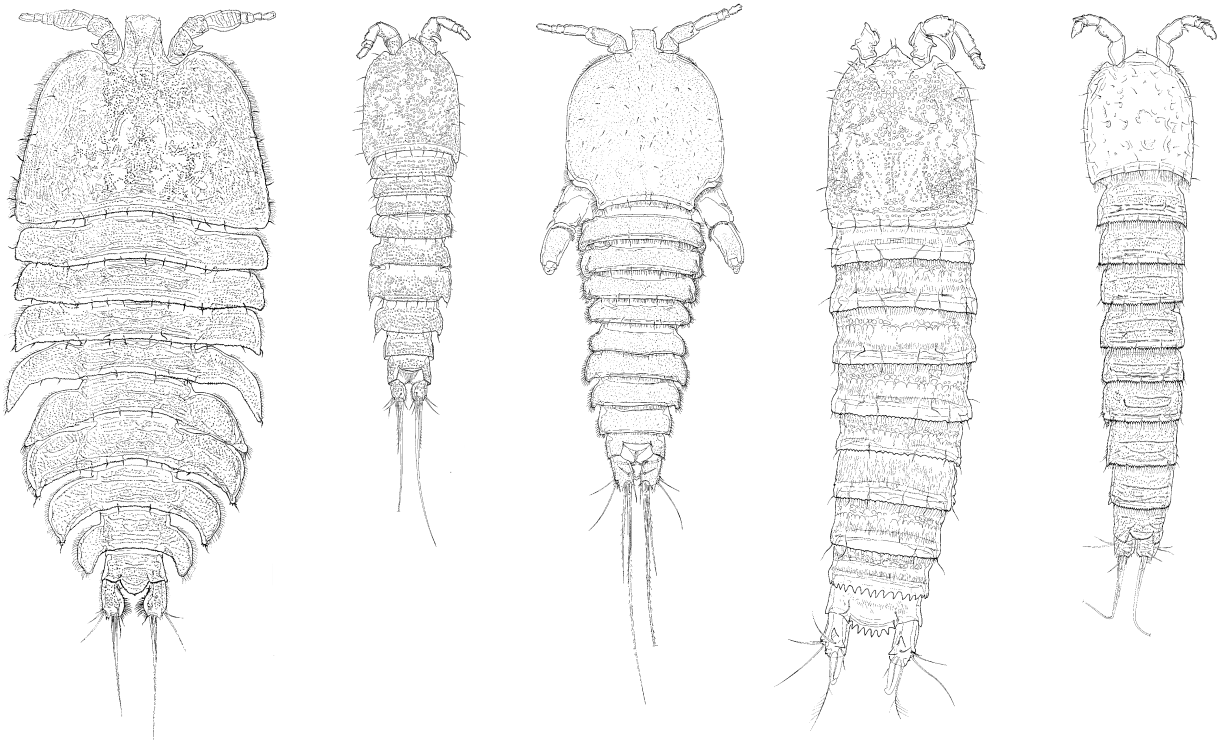
Vakgroep Biologie

Krijgslaan 281-S8, B-9000 Gent, BELGIUM

BIODIVERSITY AND TAXONOMY OF HARPACTICOID COPEPODS ASSOCIATED WITH CORAL SUBSTRATES OF TROPICS AND DEEP SEA

Biodiversiteit en taxonomie van harpacticoide copepoden geassocieerd met koraalsubstraten van tropen en diepzee



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The beginning of wisdom is getting things by their right name.

Ancient Chinese proverb

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SUMMARY

SAMENVATTING

SUMMARY

Tropical coral reefs are one of the most diverse habitats in the world's oceans. By providing substrata for sedentary organisms, and food and shelter for mobile organisms, corals create a rich series of habitats for great numbers of species (Paulay, 1996). However, the true extent of the diversity of coral reef associated organisms is still poorly understood. Best studied groups are macro- and megafauna, especially fishes and macrocrustaceans (e.g., Findley & Findley, 2001; Hughes *et al.*, 2002; Roberts *et al.*, 2002). Knowledge of the associated meiofauna (organisms between 32 μm and 1 mm) is at present limited. Nevertheless, a wide range of potential microhabitats is available for benthic fauna in the large variety of dead coral substrates, which originate from physical and biological breakdown of coral skeletons.

Although the existence of cold-water corals has been known to science since the 18th century (Pontopiddan, 1755), the occurrence, biology, and diversity of the associated communities has by no means been studied as intensively as for tropical coral reefs. Cold-water coral reefs occur in the upper bathyal zone throughout the world. Like tropical coral reefs, they are characterised by high habitat diversity (Rogers, 1999). It has even been stated that the biodiversity of *Lophelia pertusa* reefs is of a similar order of magnitude as that of some shallow-water tropical coral reefs (Rogers, 1999). Studies dealing with associated fauna on either living or dead *L. pertusa* have mainly focused on the macro- and megafauna (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999). More recently, the meiofauna (at higher taxon level) and nematofauna associated with dead coral substrates have been investigated by Raes & Vanreusel (2005, 2006).

The present study focuses on the associated harpacticoid copepod fauna of dead coral substrates. The order of Harpacticoida is one of the ten orders of the subclass Copepoda. Harpacticoid copepods are ubiquitous in marine soft-sediments and generally the second most abundant meiobenthic taxon after the numerically dominant Nematoda (Coull & Bell, 1979; Hicks & Coull, 1983; Higgins & Thiel, 1988; Giere, 1993). The associated harpacticoid assemblages of dead coral substrates are investigated in a shallow, tropical lagoon along the eastern coast of Zanzibar (Tanzania). The associated assemblages of cold-water coral substrates are investigated from *Lophelia pertusa* reefs in the Belgica Mound Province (Porcupine Seabight, NE-Atlantic), at a depth of about a 1000 m.

In **chapter 2**, the harpacticoid fauna associated with tropical coral substrates is investigated. The main aim of the study was to assess the influence of microhabitat type on assemblage structure and diversity. Three different microhabitat types were distinguished, namely dead coral fragments, coral gravel and coral sand. The coral assemblage was significantly different from that in gravel and every sediment layer, and consisted of typical 'phytal' taxa with an addition of eurytopic and sediment-dwelling forms. We assume that the sediment trapped by the coral provides a habitat for sediment-dwellers, while the complex microtopography of the coral branches provides a suitable substratum for epibenthic or even 'phytal' taxa. The assemblages of

coral gravel and upper sediment layer did not differ significantly from each other and contained mostly the same dominant genera. Differences in sediment granulometry were important in structuring the sediment assemblages. We assume that the primary factors affecting composition of the associated fauna are most likely the nature and structure of the primary substrate. Furthermore, assemblages might experience differences in environmental conditions. Especially at Makunduchi, the coral assemblage was significantly more diverse than gravel and sediment. Coral form and complexity, with implications for habitable space, nutritional resources and level of predation might be important in structuring diversity of the associated assemblage.

Chapter 3 presents the first characterisation of the harpacticoid copepod fauna associated with cold-water coral substrates. As in the previous chapter, the main aim was to assess the influence of microhabitat type on copepod assemblage structure and diversity. Three different microhabitat types were distinguished, namely dead coral fragments, glass sponge skeletons and underlying sediment. Apart from some subtle differences, it appears that coral fragments and underlying sediment do not harbour distinctly different assemblages. Only two sponge skeletons were collected and conclusions about its assemblage were considered as provisional. Several factors might be important in explaining the apparent lack of difference in assemblage structure. Sediment, retained between the coral branches, might attract sediment-dwellers, which obscure the presence of true epibenthic taxa. Active migration by swimming and the close contact between the substrates may facilitate considerable exchange. Also, the high evenness, typical of the deep sea fauna, in combination with limited sample sizes, undoubtedly influences the pattern observed. At least at the family level, the copepod fauna of the Porcupine Seabight does not seem to differ markedly from other deep-sea studies, in which essentially the same families are dominant. At the genus and species level, it is however clear that coral fragments provide a specific habitat suitable for typically 'phytal' taxa, with prehensile first legs and modified body shapes. Coral fragments and sediment were both characterised by high species diversity and low species dominance, and did not differ markedly in this. This might indicate that copepod diversity is not substantially influenced by hydrodynamical stress, which, however, is the main structuring factor of the associated nematode assemblages.

In the second part of this study, we investigate taxonomy and morphological adaptations to coral substrates within the harpacticoid family Laophontidae. This family is considered highly successful in terms of species richness and number of habitats explored. Laophontidae show a high degree of morphological plasticity and therefore are model organisms to study the relation between habitat and morphology.

In **chapter 4**, eight new species of the harpacticoid family Laophontidae, from different locations in the Indo-West Pacific Ocean, are described and placed in a new genus, *Peltidiphonte* gen. n. The new genus is clearly characterised by the extremely depressed body shape, the presence of distinct processes on the proximal antennular segments and the absence of sexual dimorphism in the endopods of the swimming legs. Most of the specimens were collected from dead coral substrates, suggesting a close affinity between the members of the new genus and this

substrate. The dorsoventral flattening of *Peltidiphonte* represents an adaptation to an epifaunal life style on the surface of dead coral fragments, and should decrease the risk of being swept away by strong currents. The new genus has a distribution covering the Indo-West Pacific Ocean. Furthermore, a key to the eight species of the genus is provided.

In **chapter 5**, two new monospecific genera of Laophontidae are established. They differ from most other laophontid genera in the absence of sexual dimorphism in the endopods of the swimming legs. Both new species resemble each other closely in habitus, integumental ornamentation, chaetotaxy of the swimming legs and absence of sexual dimorphism in the endopods. However, the detailed characteristics of A1, maxilla and male P5 show that the species are not congeneric. The new genus *Propephonte*, described from the northern coast of Papua New Guinea, is closely related to *Peltidiphonte*, based on shape and setation of the fifth pereiopods and the detailed structure of the first antennular segment. Furthermore, we assume that *Indolaophonte* and *Langia* are more derived genera within this lineage, wherein setation and segmentation of the swimming legs became more reduced as an adaptation to an interstitial life style. The new genus *Apistophonte* is described from the Kenyan coast. Based on the detailed characteristics of maxilla, fifth pereiopods and first antennular segment, we conclude that *Apistophonte* branched off from a different stock than the lineage grouping *Propephonte* and *Peltidiphonte*. The exact affinities of the genus, however, remain difficult to assess.

A new species of *Paralaophonte* is described in **chapter 6**. Its most distinguishing feature is the robust, enlarged and specialised maxilliped, formerly unseen in *Paralaophonte*. *Paralaophonte harpagone* sp. n. does not show any sexual dimorphism in the endopodite of P3 nor in the exopodites of P2 to P4. However, it is a true representative of the genus *Paralaophonte* by the typical sexually dimorph P2 endopodite with its modified distal inner seta on the second endopodal segment. The maxilliped is similar in robustness and position to the highly specialised maxilliped of the genus *Namakosiramia* Ho & Perkins, 1977, of which the two members exist as ectoparasites on holothurians. This similarity is attributed to convergence and we can only speculate whether the specialised maxilliped of *Paralaophonte harpagone* sp. n. is an adaptation to live as an associate of another invertebrate.

In **chapter 7**, a new monospecific genus, *Spiniferaphonte*, is described from coral gravel along the Kenyan coast and is particularly characterised by strong hook-like processes on the caudal rami. The new genus is closely related to *Laophontina* and *Wellsiphontina*, as shown by following synapomorphies: a denticulate operculum, a sexually dimorphic P4 exopod (reduced chaetotaxy of the ultimate segment in the male), and the absence of sexual dimorphism in the P2 and P3 endopods. The two-segmented exopod of P1 and the presence of a seta on the endopodal part of the male P5 are less derived, indicating that the new genus represents a separate lineage within this group. Interstitial genera in the Laophontidae show similar adaptations to an interstitial life style, namely a cylindrical body shape and reduced setation and segmentation of the swimming legs. Furthermore, it is striking that the presence of distinct, thorn-like processes on caudal rami is limited to interstitial genera. Distinct processes on the proximal antennular segments and a

proximally thickened caudal seta V also appear to be associated with this interstitiality. We assume that these structures may play a role in the movement and anchoring of the animals in their interstitial habitat.

Chapter 8 presents a revision of the laophontid genus *Tapholeon* Wells, 1967, which until now consisted of two species. In the present contribution, two new species are described from the coast of Kenya, *T. inconspicuus* sp. nv. and *T. tenuis* sp. n. Furthermore, a redescription of the type species *T. ornatus* Wells, 1967, based on the type material, is provided. Two species, formerly attributed to *Asellopsis* Brady & Robertson, 1873 (viz. *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), are allocated to *Tapholeon* based on the absence of sexual dimorphism in the swimming legs P2 to P4. The former of the two species is redescribed based on additional material from the Comoros. As a consequence of the transfer of these two species, the genera *Asellopsis* and *Tapholeon* have distinct distributions, with *Asellopsis* frequently reported from the Mediterranean Sea (including the Black Sea) and the eastern shores of the North Atlantic Ocean. The genus *Tapholeon* (now containing six species) shows a limited distribution confined to the southwestern part of the Indian Ocean and the Bay of Bengal. The similarities of both genera in body shape and caudal rami are attributed to convergence. An updated generic diagnosis and a key to the six species of *Tapholeon* are included.

The results of this PhD thesis demonstrate that hard coral substrates provide a specific epifaunal habitat for benthic fauna. Especially in the tropics, it has been shown that harpacticoid community structure and diversity is influenced by the presence of these degradation products. Tropical coral fragments support a specific assemblage composed of epibenthic or phytal taxa with an addition of sediment-dwelling species. The addition of microhabitats contributes significantly to total species richness. In the cold-water coral degradation zone, only small differences could be detected in harpacticoid community structure of coral fragments and underlying sediment. This may partly be due to high evenness in combination with small sample sizes, but the presence of typical 'phytal' taxa nevertheless demonstrates the importance and specific nature of the habitat provided by hard biogenic substrates in the deep sea. Harpacticoid studies of neighbouring Atlantic regions are necessary to assess the impact of cold-water coral degradation zones on regional harpacticoid diversity. Especially in the tropical lagoon, it was demonstrated that coral substrates provide a variety of habitats exploited by different Laophontidae with specialised morphologies. This family shows a high degree of morphological plasticity and certain adaptations to the habitat clearly have evolved several times independently. The number of new taxa found, in the lagoon on Zanzibar and the cold-water coral degradation zone in the Porcupine Seabight, is a clear indication of our insufficient knowledge of copepod diversity in the tropics and the deep sea.

SAMENVATTING

Tropische koraalriffen vormen één van de meest diverse habitats in de oceanen. Door een substraat te bieden aan sedentaire organismen, en voedsel en beschutting aan mobiele organismen, voorzien koralen een uitgebreide reeks habitats van grote aantallen soorten. De ware omvang van de diversiteit van organismen, die in associatie met koraalriffen voorkomen, is echter weinig begrepen. De best bestudeerde groepen zijn macro- en megafauna, voornamelijk macrocrustaceeën en vissen (e.g., Rogers, 1993; Findley & Findley, 2001; Hughes *et al.*, 2002; Roberts *et al.*, 2002). De kennis van de geassocieerde meiofauna (organismen tussen 32 µm en 1 mm) is beperkt. Voor de bodemfauna is er nochtans een uitgebreide reeks microhabitats beschikbaar in de grote variëteit van dode koraalsubstraten, die ontstaan door fysische en biologische afbraak van koraalskeletten.

Alhoewel het bestaan van koudwater-koralen gekend is sinds de achttiende eeuw (Pontopiddan, 1755), is het voorkomen, biologie, en diversiteit van de geassocieerde organismen niet zo intensief bestudeerd als in tropische koraalriffen. Koudwater-koraalriffen komen wereldwijd voor in de bovenste bathyale zone en zijn, zoals tropische koraalriffen, gekenmerkt door een hoge habitatdiversiteit (Rogers, 1999). Er werd zelfs gesuggereerd dat de biodiversiteit van *Lophelia pertusa* riffen van een zelfde grootte-orde zou zijn als die van sommige tropische koraalriffen (Rogers, 1999). Studies van de geassocieerde fauna hebben zich meestal toegespitst op de mega- en macrofauna (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999). Recent werden de geassocieerde meiofauna (op hoger taxonniveau) en de nematofauna bestudeerd door Raes & Vanreusel (2005, 2006).

Deze studie richt de aandacht op de harpacticoide copepoden-fauna geassocieerd met dode koraalsubstraten. De orde der Harpacticoida vormt één van de tien ordes binnen de Copepoda. Deze groep is alomtegenwoordig in mariene sedimenten en is het tweede meest abundante taxon na de Nematoda (Coull & Bell, 1979; Hicks & Coull, 1983; Higgins & Thiel, 1988; Giere, 1993). De harpacticoide gemeenschappen geassocieerd met dode koraalsubstraten werden onderzocht in een ondiepe, tropische lagune langs de oostelijke kust van Zanzibar (Tanzania). De gemeenschappen geassocieerd met koudwater-koraalsubstraten werden bestudeerd in de Belgica Mound regio van de Porcupine Seabight (Noord-Oost Atlantische Oceaan), op een diepte van ongeveer 1000 meter.

In **hoofdstuk 2** wordt de harpacticoidenfauna, geassocieerd met tropische koraalsubstraten, bestudeerd. Het belangrijkste doel van deze studie was het inschatten van de rol van het type microhabitat in het beïnvloeden van gemeenschapsstructuur en diversiteit. Drie verschillende microhabitat types werden onderscheiden, namelijk dode koraalfragmenten, koraalgruis en koraalzand. De koraalgemeenschap was significant verschillend van gruis en elke sedimentlaag, en bestond voornamelijk uit zogenaamd epifytische taxa met een aanvulling van eurytopische en sediment-bewonende vormen. Wij nemen aan dat het sediment, dat zich tussen de koraaltakken bevindt, een habitat biedt voor sedimentbewoners. De complexe microtopografie van de

koraaltakken vormen een geschikt substraat voor epibenthische of zelfs epifytische taxa. De gemeenschappen van koraalgruis en bovenste sedimentlaag verschilden niet significant van elkaar en deelden de meeste dominante genera. Verschillen in sediment karakteristieken waren belangrijk in het structureren van de sedimentgemeenschappen. We nemen aan dat de belangrijkste factoren, die de samenstelling van de geassocieerde fauna beïnvloeden, de eigenschappen en struktuur van het substraat zijn. Verder is het mogelijk dat de gemeenschappen verschillen in milieu-omstandigheden waarnemen. Voornamelijk in Makunduchi was de koraalgemeenschap significant meer divers dan koraalgruis en sediment. We nemen aan dat de vorm en complexiteit van het koraal, met gevolgen voor de beschikbare ruimte, beschikbaarheid van voedsel en bescherming tegen predatie, belangrijk zijn in het structureren van de diversiteit van de geassocieerde gemeenschap.

Hoofdstuk 3 stelt de eerste karakterisatie voor van de harpacticoiden geassocieerd met koudwaterkoraal-substraten. Zoals in het vorige hoofdstuk, was de belangrijkste doelstelling het onderzoeken van de invloed van het type microhabitat op gemeenschapsstructuur en diversiteit. Drie verschillende microhabitat types werden onderscheiden, dode koraalfragmenten, glassponsskeletten en het onderliggende sediment. Afgezien van enkele subtiele verschillen, lijken koraalfragmenten en onderliggend sediment geen duidelijk verschillende gemeenschappen te herbergen. Slechts twee sponsskeletten werden verzameld en bijgevolg werden conclusies over de geassocieerde gemeenschap als voorbarig beschouwd. Verschillende factoren kunnen belangrijk zijn in het verklaren van de schijnbare afwezigheid van verschillen in gemeenschapsstructuur. Het sediment tussen de koraaltakken kan sedimentbewoners aantrekken die de aanwezigheid van echte epibenthische taxa verdoezelen. Actieve migratie door zwemmen en het nauwe contact tussen de substraten kan aanzienlijke uitwisseling mogelijk maken. Ongetwijfeld beïnvloedt de hoge equitabiliteit, die typisch is voor de diepzee, in combinatie met de beperkte staalgroottes het patroon dat geobserveerd werd. Op familieniveau lijkt de copepodenfauna van de Porcupine Seabight niet duidelijk te verschillen van andere diepzeestudies waar in hoofdzaak dezelfde families dominant zijn. Op genus- en soortsniveau is het echter duidelijk dat koraalfragmenten een specifiek habitat bieden voor typisch epifytische taxa, met prehensiele eerste potenparen en aangepaste lichaamsvormen. Koraalfragmenten en sediment worden beiden gekenmerkt door hoge soortenrijkdom en equitabiliteit en verschillen hierin niet duidelijk van elkaar. Dit kan erop wijzen dat de diversiteit van copepoden niet duidelijk beïnvloed wordt door verstoring door waterstromingen, die echter de belangrijkste structurerende factor is van de geassocieerde nematodengemeenschappen.

In het tweede deel van deze studie worden taxonomie en morfologische aanpassingen aan koraalsubstraten onderzocht binnen de harpacticoide familie Laophontidae. Deze familie is soortenrijk en komt voor in een groot aantal habitats. Laophontidae vertonen een grote morfologische plasticiteit en zijn daarom modelorganismen om de relatie tussen habitat en morfologie te bestuderen.

In **hoofdstuk 4** worden acht nieuwe soorten van de familie Laophontidae beschreven van verschillende locaties in de Indo-West Pacifische Oceaan en in een nieuw genus geplaatst, genaamd *Peltidiphonte*. Het nieuwe genus wordt duidelijk gekenmerkt door de extreem afgeplatte lichaamsvorm, de aanwezigheid van karakteristieke uitsteeksels op de proximale segmenten van de eerste antenne en de afwezigheid van seksueel dimorfisme in de endopodieten van de zwempoten. De meeste specimens werden van dode koraalsubstraten verzameld wat wijst op een nauwe affiniteit tussen de vertegenwoordigers van het genus en dit substraat. De dorsoventrale afplatting van *Peltidiphonte* stelt een adaptatie voor aan een epifaunale levenswijze op het oppervlak van dode koraalfragmenten. De afplatting zou voornamelijk de kans verminderen om weggespoeld te worden door sterke stromingen. Het nieuwe genus heeft een verspreiding die de Indo-West Pacifische Oceaan omvat. Tenslotte wordt een sleutel voor de acht soorten van het genus gegeven.

In **hoofdstuk 5** worden twee nieuwe monospecifieke genera opgericht. Ze verschillen van de meest andere laophontide genera in de afwezigheid van seksueel dimorfisme bij de endopodieten van de zwempoten. Beide nieuwe soorten lijken sterk op elkaar in lichaamsvorm, lichaamsornamentatie, bevering van de zwempoten en afwezigheid van seksueel dimorfisme in de endopodieten. De gedetailleerde karakteristieken van antennule, maxilla en mannelijke vijfde pereiopode wijzen erop dat deze twee soorten niet nauw verwant zijn. Het nieuwe genus *Propephonte*, beschreven van de noordelijke kust van Papua New Guinea, is nauw verwant met *Peltidiphonte*, gebaseerd op vorm en bevering van de vijfde pereiopoden en de gedetailleerde structuur van het eerste segment van de antennule. Er wordt verder verondersteld dat *Indolaophonte* en *Langia* meer afgeleide genera zijn, waarbij bevering en segmentatie van de zwempoten meer gereduceerd werd als een aanpassing aan een interstitiële levenswijze. Het nieuwe genus *Apistophonte* wordt beschreven van de Keniaanse kust. Gebaseerd op de gedetailleerde kenmerken van maxilla, vijfde pereiopoden en eerste segment van de antennule, wordt er besloten dat *Apistophonte* een andere lijn vertegenwoordigt dan de lijn die *Propephonte* en *Peltidiphonte* groepeert. De exacte verwantschappen van dit genus zijn echter moeilijk in te schatten.

Een nieuwe soort binnen het genus *Paralaophonte* wordt beschreven in **hoofdstuk 6**. Het meest opvallende kenmerk is de robuuste, vergrootte en gespecialiseerde maxillipede, nieuw binnen het genus. *Paralaophonte harpagone* sp. n. vertoont geen seksueel dimorfisme in de endopodiet van de derde pereiopode noch in de exopodieten van de tweede tot vierde exopodieten. Deze soort is echter een duidelijke vertegenwoordiger van het genus *Paralaophonte* door de typisch seksueel dimorfe endopodiet van de tweede pereiopode met een gemodifieerde distale binnenste seta op het tweede segment. De maxillipede is vergelijkbaar in robuustheid en positie met de sterk gespecialiseerde maxillipede van het genus *Namakosiramia* Ho & Perkins, 1977, waarvan de twee vertegenwoordigers als ectoparasieten voorkomen op zeekomkommers. De gelijkenis wordt toegeschreven aan convergentie en men kan enkel speculeren of de

gespecialiseerde maxillipede van *Paralaophonte harpagone* sp. n. een aanpassing is om geassocieerd te leven met een andere ongewervelde.

In **hoofdstuk 7** wordt een monospecifiek genus, *Spiniferaphonte*, beschreven van koraalgruis langs de Keniaanse kust. Het genus wordt voornamelijk gekenmerkt door sterke haakvormige uitsteeksels op de caudale rami. Het nieuwe genus is nauw verwant met *Laophontina* en *Wellsiphontina*, zoals getoond door volgende synapomorfieën: een getand operculum, een seksueel dimorfe exopodiet van de vierde pereiopode (gereduceerde bevering van het laatste segment), en de afwezigheid van seksueel dimorfisme in de endopodieten van de tweede en derde pereiopoden. De exopodiet van de eerste pereiopode, bestaande uit twee segmenten, en de aanwezigheid van een seta op het deel van de endopodiet van de mannelijke vijfde pereiopode wijzen erop dat het nieuwe genus een afzonderlijke lijn binnen deze groep vertegenwoordigt. Interstitiële genera binnen de Laophontidae vertonen vergelijkbare aanpassingen (aan een interstitiële levenswijze), namelijk een cilindrische lichaamsbouw en een gereduceerde bevering en segmentatie van de zwempoten. Verder is het opvallend dat de aanwezigheid van duidelijke, doornvormige uitsteeksels op de caudale rami beperkt is tot interstitiële genera. Duidelijke uitsteeksels op de proximale segmenten van de antennule en een proximaal verdikte caudale seta V lijken ook geassocieerd te zijn met deze interstitiële levenswijze. Deze structuren kunnen een rol spelen bij de beweging en verankering van de dieren in het interstitieel habitat.

Hoofdstuk 8 is een revisie van het laophontide genus *Tapholeon* Wells, 1967, dat tot op heden uit twee soorten bestond. In deze studie worden twee nieuwe soorten beschreven van de Keniaanse kust, *T. inconspicuus* sp. n. en *T. tenuis* sp. n. Verder gebeurt een herbeschrijving van de typesoort, *T. ornatus* Wells, 1967, gebaseerd op het typemateriaal. Twee soorten, voordien toegewezen aan *Asellopsis* Brady & Robertson, 1873 (viz. *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), worden overgebracht naar *Tapholeon* op basis van de afwezigheid van seksueel dimorfisme in de tweede tot vierde zwempoten. De eerste van deze twee soorten wordt herbeschreven op basis van bijkomend materiaal uit de Comoren. Ten gevolge van de overdracht van deze twee soorten, hebben de genera *Tapholeon* en *Asellopsis* verschillende verspreidingsgebieden. *Asellopsis* werd frequent waargenomen van de Middellandse Zee (met inbegrip van de Zwarte Zee) en de oostelijke kusten van de Noord Atlantische Oceaan. Het genus *Tapholeon* (dat nu uit zes soorten bestaat) vertoont een beperkte verspreiding in het zuidwestelijke deel van de Indische Oceaan en de Baai van Bengalen. De gelijkenissen in lichaamsvorm en vorm van de caudale rami worden toegeschreven aan convergentie. De genus diagnose wordt aangepast en een sleutel voor de zes soorten van het genus gegeven.

De resultaten van dit doctoraal onderzoek tonen aan dat harde koraalsubstraten een epifaunaal habitat bieden van bodemfauna. In de tropen worden gemeenschapsstructuur en diversiteit van de harpacticoide copepodengemeenschappen duidelijk beïnvloed door de aanwezigheid van deze afbraakproducten. Tropische koraalfragmenten ondersteunen een gemeenschap bestaande uit epibenthische en epifytische taxa, aangevuld door sediment-bewonende soorten. Het bemonsteren van verschillende microhabitats draagt in belangrijke mate

bij tot de totale soortenrijkdom. In de koudwaterkoraal-afbraakzone werden slechts kleine verschillen waargenomen in harpacticoide gemeenschapsstructuur van koraalfragmenten en onderliggend sediment. Dit is deels te wijten aan de hoge equitabiliteit in combinatie met de beperkte staalgroottes, maar de aanwezigheid van typisch 'epifytische' taxa toont niettemin het belang en de specifieke aard van het habitat van harde biogene substraten in de diepzee aan. Studies van harpacticoide gemeenschappen in naburige regio's in de Atlantische Oceaan zijn noodzakelijk om de impact van koudwaterkoraal-afbraakzones op regionale diversiteit in te schatten. We toonden aan dat tropische koraalsubstraten een veelheid aan habitats bieden voor Laophontidae met gespecialiseerde morfologische aanpassingen. Deze familie vertoont een hoge mate van morfologische plasticiteit en bepaalde aanpassingen aan het habitat zijn duidelijk verschillende malen onafhankelijk van elkaar ontstaan. De hoge aantallen nieuwe taxa, in de lagune in Zanzibar en de koudwaterkoraal-afbraakzone in de Porcupine Seabight, wijzen erop dat onze kennis van copepoden diversiteit in de tropen en de diepzee tot op heden nog beperkt is.

CHAPTER 1

General introduction, aims and thesis outline

1 .1. FRAMEWORK

Tropical coral reefs are one of the most diverse habitats in the world's oceans. By providing substrata for sedentary organisms, and food and shelter for mobile organisms, corals create a rich series of habitats for great numbers of species. Diversity includes animals which are obligate reef associates and many animals which occur in both reef and non-reef environments (Paulay, 1996). However, the true extent of the diversity of coral reef associated organisms is still poorly understood. Best studied groups are macro- and megafauna, especially fishes and macrocrustaceans (e.g., Rogers, 1993; Findley & Findley, 2001; Hughes *et al.*, 2002; Roberts *et al.*, 2002). Tropical coral reefs are characterised by high spatial heterogeneity in community structure and marked patchiness in species distributions. They show a high degree of spot endemism and high number of rare species (Cornell & Karlson, 1996; Edmunds & Bruno, 1996; Small *et al.*, 1998; Schlacher *et al.*, 1998). The diversity of local coral assemblages is strongly related to regional differences in species richness. Thus, local diversity patterns are influenced by more than local environmental factors and a broader regional perspective is required to understand them (Cornell & Karlson, 1996; Karlson & Cornell, 1998; Karlson *et al.*, 2004).

Although the existence of cold-water corals has been known to science since the 18th century (Pontopiddan, 1755), the occurrence, biology, and diversity of the associated communities has by no means been studied as intensively as for tropical coral reefs. Recently, the improvement of sampling methods has increased our knowledge of these deep-water reefs. Cold-water coral reefs occur in the upper bathyal zone throughout the world. Like tropical coral reefs, they are characterised by high habitat diversity (Rogers, 1999). Furthermore, it has been stated that the biodiversity of *Lophelia pertusa* reefs seems of a similar order of magnitude as that of some shallow water tropical coral reefs (Rogers, 1999). Studies dealing with associated fauna on either living or dead *L. pertusa* have mainly focused on the macro- and megafauna (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999). More recently, the meiofauna (at higher taxon level) and nematofauna associated with dead coral substrates has been investigated by Raes & Vanreusel (2005, 2006). They found that the presence of large biogenic structures particularly favours harpacticoid copepods as in the meio-epifaunal community this taxon has a higher relative abundance than in the underlying sediment.

The order of Harpacticoida is one of the ten orders of the subclass Copepoda. They are ubiquitous in marine soft-sediments and generally the second most abundant meiobenthic taxon after the numerically dominant Nematoda (Coull & Bell, 1979; Hicks & Coull, 1983; Higgins & Thiel, 1988; Giere, 1993). This ubiquity extends into deep-sea environments where they have proportionally increasing abundance compared to macrobenthos (Thistle, 2001) and exhibit high diversity (Coull, 1972; Thistle, 1978). Harpacticoids have the ability to inhabit multiple habitat types. They show a high level of habitat specificity and adaptations to their environment (Hicks & Coull, 1983; Huys & Boxshall, 1991; Dahms & Qian, 2004), which is reflected in a high diversity of body forms (Remane, 1952; Noodt, 1971). Harpacticoids play an important trophic role because of their numerical abundance, capacity to recycle nitrogen and high bacterial

ingestion rates (Gray, 1985; Moriarty *et al.*, 1985). They further are an important food source for larval, juvenile and small fishes (Gee, 1989; Coull, 1990; De Troch *et al.*, 1998).

The present study fits in the frame of FWO research project G.0199.03, 'A Comparative Study of the Meio-Epifauna Associated with Tropical and Cold-Water Coral Reefs', which aimed to analyse the importance of local factors and regional processes for biodiversity of the associated meio-epifauna of tropical and cold-water coral substrates. The associated nematofauna has recently been dealt with in the doctoral study of Dr. M. Raes (2006).

1.2. HARPACTICOID COPEPODS IN TROPICAL REEF LAGOONS

Despite the considerable research effort on the meiofauna communities associated with carbonate reef sediments, studies have primarily focused on the nematode benthic assemblages and generally ignored the meiofauna living as epifauna on the hard coral substrates. Soft-bottoms constitute large areas in most lagoons, sometimes covered by seagrass beds. The carbonate sands result from the mechanical degradation and bioerosion of coral heads and reef structures (Le Campion-Alsumard *et al.*, 1993; Peyrot-Clausade *et al.*, 1995) and further contain mollusc and crustacean shells, coralline algae, *Halimeda* debris and foraminiferan and radiolarian tests (Chevillon, 1996; Villiers & Bodiou, 1996). Most of the tropical meiofauna studies have been carried out in the South Pacific, in French Polynesia (Salvat & Renaud-Mornant, 1969; Renaud-Mornant *et al.*, 1971; Thomassin *et al.*, 1982; Gourbault & Renaud-Mornant, 1989; Gourbault & Renaud-Mornant, 1990; Boucher *et al.*, 1998), Great Barrier Reef (St.John *et al.*, 1989), Fiji (Boucher & Kotta, 1996) or Costa Rica (Guzmán *et al.*, 1987). Only two studies were carried out in the North Atlantic on Bermuda (Coull, 1970) and Guadeloupe (Boucher & Gourbault, 1990), two in the South Atlantic on Rocas Atoll (Netto *et al.*, 1999a; Netto *et al.* 2003), three in the Red Sea (Grelet, 1984; Grelet *et al.*, 1987; Arlt, 1995) and four in the Indian Ocean on Madagascar (Thomassin *et al.*, 1976) and Zanzibar (Ólafsson *et al.*, 1995; Ndaro & Ólafsson, 1999; Raes *et al.*, 2007). These investigations have mostly been conducted in the shallow subtidal of the reef lagoon, which is the focus of chapter 2 in the present study.

The ecology of harpacticoid communities has been studied in a wide range of habitats in temperate and subtropical seas (Hicks & Coull, 1983). In contrast, little is known of the harpacticoids inhabiting the carbonate sands of coral reefs, with most of the studies focused on taxonomy (e.g. Sewell, 1940; Chappuis, 1954 (Madagascar); Krishnaswamy, 1957 (India); Vervoort, 1964 (Caroline Islands); Wells, 1967 (Mozambique); Bozic, 1969 (Réunion); Wells & McKenzie, 1973 (Seychelles); Mielke, 1981 (Galapagos); Wells & Rao, 1987 (Andaman & Nicobar Islands); Fiers & De Troch, 2000 (Kenya)). Up to now, there is only scant information on harpacticoid assemblage structure, from a few geographically disjunct areas, namely the Bermuda Platform (Coull, 1970; Coull & Herman, 1970), the U.S. Virgin Islands (Hartzband & Hummon, 1974), and Mururoa (Villiers *et al.*, 1987; Villiers, 1988) and Fangataufa Atoll (Villiers & Bodiou, 1996), both in French Polynesia.

Meiofauna composition, density and diversity

Sediment granulometry, with its effect on other parameters of the environment, is generally recognised as a major structuring factor of meiofauna populations in coral reef sediments (Gourbault *et al.*, 1995; Ólafsson, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999). Granulometry is mainly influenced by physical factors but macrofaunal bioturbation and disturbance due to feeding and locomotion can also modify sediment structure, giving rise to a patchy distribution of meiobenthos (Ndaro & Ólafsson, 1999). Both horizontal and vertical distribution further depend on biological interactions, availability of food and oxygen and other physico-chemical factors such as turbulence, temperature and organic matter (Hicks & Coull, 1983; Decho *et al.*, 1985). Several of these factors are interrelated to each other as increased hydrodynamical stress will result in better sorted, coarser sediment with lower clay-silt content and less accumulation of organic matter. Several studies demonstrated a dominance of nematodes in the sheltered zones of the reef, where accumulation of detritus occurs and the sediment consists of fine sands with higher silt contents. In coarser and better sorted sediments, evidencing a high energy environment, copepod dominance generally increases (Thomassin *et al.*, 1982; Gourbault & Renaud-Mornant, 1989; St.John *et al.*, 1989; Gourbault & Renaud-Mornant, 1990). Furthermore, Coull (1970) found that as the grain size at a site in Bermuda switched seasonally from fine to coarse, numerical dominance switched from nematodes to copepods. Gourbault & Renaud-Mornant (1990) however found an unexpectedly high dominance of copepods (44 %) in the silt-rich deep area of the lagoon at Fangataufa Atoll, and explained this as an opportunistic colonisation by eurytopic and highly tolerant species. These findings generally support the trend that harpacticoids dominate or become numerically more abundant as the particle size of the sediment increases (Hicks & Coull, 1983). Harpacticoids are typically the most sensitive meiofaunal taxon to decreasing oxygen tension (Moodley *et al.*, 1997; Wetzel *et al.*, 2001) and the degree of oxygenation is evidently better in coarser sediments. Fine sediments should particularly favour nematodes which generally exhibit a high tolerance to oxygen deficiency. Also, permeability and porosity should be higher in coarse carbonate sediments. These two properties affect the distribution and abundance of infaunal organisms because they restrict water exchange and the organisms' capacity for movement in the interstitial spaces (Pollock, 1971; Gray, 1974). Gourbault & Renaud-Mornant (1990) showed that nematode dominance increased in deeper layers while copepod percentages decreased. Coull (1970) attributed the reduction of copepods in deeper sediment layers to decreased interstitial water and oxygen content.

Meiobenthos abundance is particularly determined by the quantity of organic matter in the sediment (Gómez Nogueira & Hendrickx, 1997; Coull, 1999). Favourable nutritive conditions, e.g. in sheltered zones where detritus accumulates and is not eroded away by the flow regime, should result in increased benthic abundance (Gamenick & Giere, 1994). The detritus available may be derived from a variety of sources including the reef-flat (considered the most productive zone of the reef (Kinsey, 1985)), in situ benthic production as well as derived from the water column biota (Netto *et al.*, 2003). Several studies have recorded highest meiofauna densities in

fine sands (Alongi, 1989b; Grelet *et al.*, 1987; Gourbault *et al.*, 1995; Boucher, 1997; Gómez Noguera & Hendrickx, 1997), which might reflect lower hydrodynamical stress and accumulation of detritus. According to several authors, the seasonality in abundance of most meiofaunal taxa in tropical inter- and subtidal areas is closely related to monsoons (Ganapati & Rao, 1962; Kondalarao & Ramana Murty, 1988; Alongi, 1990), which applies especially to the 'wet' tropics.

Diversity of the meiofauna assemblage is also related to sediment characteristics in that a heterogeneous mixture of fine and coarse sediments offers more potential niches than homogeneous sediments (Gray, 1981; Gray, 2002). Further, a certain degree of disturbance by hydrodynamic stress might lead to lower density but an increase in diversity, because of lower competition for resources (Netto *et al.*, 1999a). Netto *et al.* (1999b) found higher diversity at the sheltered sites of a carbonate intertidal flat and related this to the structural complexity of the habitats, the increase of sediment stability and the fact that these sites accumulated organic matter more than in exposed areas.

Harpacticoid composition, density and diversity

Due to the limited information, available from a few geographically disjunct areas (Table 1), it is at present difficult to reveal general patterns concerning harpacticoid composition and diversity in the carbonate sands of coral reefs. However, the available studies generally found that assemblage structure is mainly determined by sediment granulometry as controlled by reef hydrodynamics. Information on diversity, density and dominant families (or genera) of harpacticoid copepods in tropical lagoons is summarized in Table 2.

		Region	Location	Habitat
1	Coull (1970)	North Atlantic	Bermuda	platform
2	Hartzband & Hummon (1974)	Carribean Sea	St. Thomas (U.S. Virgin Islands)	shallow subtidal of patch reef
3	Villiers *et al.* (1987)	South Pacific	Mururoa	coral reef lagoon (atoll)
4	Villiers & Bodiou (1996)	South Pacific	Fangataufa	coral reef lagoon (atoll)

Table 1. Sampling locations of the harpacticoid copepod studies considered in Chapter 1.2.

Coull (1970) distinguished three harpacticoid communities which were similar to assemblages in similar sediment types from other parts of the world, representing isocommunities *sensu* Thorson (1957). A typical sublittoral mud community was dominated by representatives of *Stenhelia*, *Enhydrosoma*, *Cletodes* and *Typhlamphiascus*. The medium to coarse sands were highly dominated by a species of *Phyllopodopsyllus* (Tetragonicipitidae) which is typical for any coarse shell-gravel (carbonate) assemblage (Hicks & Coull, 1983). The third assemblage, in the submerged 'beach sands', consisted of typical interstitial harpacticoids (*Leptastacus*, *Praeleptomesochra*). Coull & Herman (1970) further stated that the distribution of the shell bottom fauna (typically with representatives of Tetragonicipitidae, *Robertgurneya*, *Rhyncholagena*, *Orthopsyllus*,

Paralaophonte) is restricted to those warm temperate, tropical or semi-tropical carbonate sediments of biogenic origin, in contrast to the worldwide distribution of the mud and psammic communities. Harpacticoid community structure of the lagoon at Fangataufa Atoll (French Polynesia) also appears to be determined primarily by sediment granulometry as controlled by reef hydrodynamics (Villiers & Bodiou, 1996). The central deep zone harbours an assemblage of epibenthic sand-dwelling forms (mainly Diosaccidae which is also the most dominant family) associated with silty fine sands, including typical burrowers (e.g. *Enhydrosoma*). The assemblages at the inner periphery of the lagoon are less homogeneous and consist of species typical of coarse sands at the littoral fringe (e.g. *Bulbamphiascus*, *Phyllopodopsyllus*). The neighbouring atoll of Mururoa differs in the high percentage of interstitial and gravel-dwelling species which is due to the medium-grained well sorted sands (Villiers *et al.*, 1987). The irregular carbonate grains of biogenic origin allow for increased interstitial space, which particularly favours interstitial copepods. If the spaces are filled with small mineral and detrital particles, however, the closure of the interstitial space eliminates many interstitial forms (Renaud-Debyser, 1963).

Coull (1970) observed distinct seasonal patterns, with copepod abundance related to reproductive cycles and changing sediment conditions. Lowest abundances were observed when water temperature was lowest.

	Number of families	Number of genera	Number of species	*H'* (species)	*J'*	Dominant families / genera	Harpacticoid densities (ind./10 cm²)
1		45	61				6-967 (adults + copepodites)
2		25	33	0,9-3,3		*Robertgurneya* (34%), *Normanella* (15,8%), *Dactylopusia* (7,2%), *Paralaophonte* (7,2%), *Laophonte* (6,9%)	5-42 (adults)
3	12	40	57	2,54-4,22	0,68-0,88	Diosaccidae (69%), Ameiridae (14,3%), Paramesochridae (6,5%)	1-292 (adults + copepodites)
4	10	31	42	2,2-3,80	0,6-0,89	Diosaccidae (69,1%), Ameiridae (15,9%), Canthocamptidae (5,5%)	

Table 2. Family, genus and species richness, dominance, dominant families (or genera) and densities of harpacticoids in tropical lagoons. Numbers in first column represent the sampling locations given in Table 1. Note that families and genera are according to systematics of the time.

Coull (1970), Hartzband & Hummon (1974) and Villiers & Bodiou (1996) related diversity of the assemblages to the amount of hydrodynamical stress. Generally, higher diversity and equitability was encountered in the calm, silty sediments typical of homogeneous, stable physical and chemical conditions. Villiers & Bodiou (1996) found species diversity and equitability positively correlated to the silt content of the sand. Less stable, variable assemblages with higher dominance were found in areas of greater environmental constraints (e.g. exposure to wave action, bioturbation, currents). Both Coull (1970) and Hartzband & Hummon (1974) related these patterns to the stability-time hypothesis of Sanders (1968), in which a community in stable physical conditions is regulated mainly by biological interactions and not by physiological stress,

subsequently attaining a high diversity. On the other hand, Boucher & Gourbault (1990) stated that tropical coral ecosystems are thought to be non-equilibrium systems (Connell, 1978), in which frequent disturbances may limit competitive dominance and favour the establishment of a diverse community.

Cryptofauna of coral heads

Up to now, studies of the associated fauna of large coral fragments or coral heads have mainly focused on the associated crustaceans as a group (regardless of size). Variously described as microcrustaceans (e.g. Klumpp *et al.*, 1988) or cryptofauna (e.g. Peyrot-Clausade, 1980; Preston & Doherty, 1994), this group consists of copepods, amphipods, ostracods, cumaceans, tanaids and isopods, and occupies an important position near the bottom of various food chains within the reef environment (Klumpp *et al.*, 1988; Hobson, 1991; Preston & Doherty, 1994). Although copepods (mainly consisting of harpacticoids) are mostly the dominant group (Klumpp *et al.*, 1988; Preston & Doherty, 1994; Nogueira, 2003), knowledge of their composition and diversity is at present lacking.

Several studies have suggested that size of the coral-head is positively correlated with cryptofaunal species richness and abundance (Austin *et al.*, 1980; Coles, 1980; Huber & Coles, 1986). However, this is not a general trend (Gotelli *et al.*, 1985) which implies that additional habitat factors might be more important than size of the coral-head alone (Edwards & Emberton, 1980). Hermatypic corals represent discrete microhabitats that vary in complexity according to species and branching pattern. Coral form further creates variations in the physical environment that may have potentially important implications for the associated epifaunal organisms, including (1) increased refuge from predation (Bell & Woodin, 1984; Sebens, 1984; Vytopil & Willis, 2001); (2) increased potential for niche separation (Begon *et al.*, 1990; Schluter & Ricklefs, 1993); and (3) increased modification of the local hydrodynamic environment (Helmuth *et al.*, 1997). Alteration of water flow may enhance or reduce delivery of organic matter, with implications for the nutritional resources available (Vytopil & Willis, 2001). At present, there is however scant information on the structuring role of these physical attributes of the coral habitat. Lewis & Snelgrove (1990) demonstrated that crustacean cryptofaunal abundance responds to different growth forms of one species of hermatypic coral (*Madracis mirabilis*), with fewer copepods on corals with short, widely separated branches than on those with long, thin, tightly spaced branches. These tightly spaced branches also contained relatively less live tissue per branch. Larger crustaceans tend to be obligate symbionts and hence are more abundant in habitats with a high proportion of live coral tissue (Coles, 1980). The smaller crustaceans (copepods and isopods) tended to be more abundant in sites with less live coral tissue where other food sources are likely to be available (Lewis & Snelgrove, 1990). Thus, a combination of spatial separation of the branches as well as food availability and preferences may be important in structuring the cryptofaunal composition. A more tightly branched coral structure has also been linked with an increased protection against predation (Vytopil & Willis, 2001).

In reef environments, the disintegration of solid biogenic structures is accomplished by biological and physical processes (Sammarco, 1996). Coral skeletons are penetrated by boring organisms and eroded away at rates that are related to exposure (Coles, 1980; Hutchings *et al.*, 1992; Scoffin, 1992). Preston & Doherty (1994) explained a dramatic decline in copepod abundance as a response to this habitat loss. However, coral skeletons are also colonised by filamentous algae and other epiphytes, which increase microhabitat diversity and may compensate for the habitat loss due to bioerosion. Different studies have demonstrated a close relation of cryptofaunal abundance with density of these filamentous algae (Lobel, 1980; Klumpp *et al.*, 1988), rather than to the complexity of the coral substratum. The amount and type of sediment which accumulates between the dead coral branches also appears to be an important determinant of abundance and composition of the associated cryptofauna (Preston & Doherty, 1994).

1.3. HARPACTICOID COPEPODS OF THE DEEP SEA

The deep-sea floor, although comprising over 50% of the earth's surface (Tyler, 2003), has to be considered as terra incognita with respect to benthological research (George, 2004). At present, studies on the composition, distribution and diversity of deep-sea harpacticoid communities at the species level are scarce (e.g. Drzycimski, 1969; Coull, 1972; Hessler & Jumars, 1974; Thistle, 1978, 1998; Thistle *et al.*, 1993; Rose *et al.*, 2005; Baguley *et al.*, 2006). Because of high species diversity and low species dominance, most qualitative or quantitative studies have either concentrated on single or few subgroups (e.g. Bodin, 1968; Por, 1969; Becker & Schriever, 1979; Thistle & Eckman, 1988; Huys & Thistle, 1989; George 1999; George & Schminke, 2002) or were restricted to supraspecific taxa (e.g. Tietjen, 1992; Vincx *et al.*, 1994; Vanhove *et al.*, 1995; George & Schminke, 1999; Ahnert & Schriever, 2001). Also, as usually at least 95% of Harpacticoida from benthic deep-sea samples are new to science (Thistle, 1998) and the systematics of the described species are in a state of flux, species level analyses are difficult and time-consuming (Seifried, 2004).

The composition, density and diversity of the meiobenthos of the deep North-East Atlantic has been reviewed by Vincx *et al.* (1994). However, as already mentioned by Vincx *et al.* (1994), no complete diversity analysis has been made of the deep-sea copepod communities. Nevertheless, some taxonomic studies have been performed, e.g. in the deep sea of the Bay of Biscay (Bodin, 1968; Dinet, 1977, 1981), the Iceland-Faroe Ridge (Schriever, 1983, 1984) and in the fjords near Bergen (Norway) (Por, 1965; Drzycimski, 1969), suggesting a diverse assemblage with many undescribed species. Recently, Seifried (2004) summarised the knowledge of systematics, abundance, diversity and distribution of deep-sea species of Harpacticoida and stressed the importance of a phylogenetic system for the study of deep-sea diversity. In the following, information is assembled from Seifried (2004) supplemented with information from other deep-sea studies.

Harpacticoid composition

Vincx *et al.* (1994) reported harpacticoid assemblages in the North-East Atlantic deep sea as dominated by Cletodidae, Diosaccidae, Ectinosomatidae, Tisbidae and Cerviniidae. However, at the time, certain genera were assigned to different families. Several genera, formerly assigned to Cletodidae, now belong to different families (Argestidae, Canthocamptidae, Huntemanniidae and Pseudotachidiidae). Former genera of Tisbidae *sensu* Lang (1944), have recently been moved to Neobradyidae, Idyanthidae and Zosimidae by Seifried (2003). As a consequence, Tisbidae *sensu* Seifried (2003) now are extremely rare in the deep-sea benthos (Seifried, 2004). Also, sample processing and sampling methods should be taken into account when comparing studies. For example, in Por (1969) and Coull (1972) the pronounced occurrence of Aegisthidae, the former Cerviniidae Sars, 1905 (Seifried & Schminke, 2003), is due to the sampling methods used, as most of its species belong to the epi- or hyperbenthic fauna (Seifried, 2004).

Nevertheless, it appears that the deep-sea fauna is typically dominated by certain families, namely Ameiridae, Argestidae, Ectinosomatidae, Pseudotachidiidae *sensu* Willen (2000), Neobradyidae *sensu* Seifried (2003) and Zosimidae (Seifried, 2004). Ahnert & Schriever (2001) reported Ameiridae, Ectinosomatidae, Argestidae, Tisbidae (majority of the specimens belonging to *Zosime* and *Pseudozosime*) and Neobradyidae as the dominant families in the deep sea of the SE Pacific ocean. George & Schminke (2002) found Paramesochridae, Ectinosomatidae, Diosaccidae and Tisbidae as the most abundant families from the Great Meteor Seamount, which reaches to about 270 m of water depth in the subtropical North Atlantic. In Sagami Bay (central Japan, at 1430 m depth), Miraciidae, Ectinosomatidae, Ameiridae and Tisbidae (with species of *Idyellopsis* and *Zosime*, which now belong to Idyanthidae and Zosimidae, respectively) were the most abundant of the 13 harpacticoid families observed (Shimanaga *et al.*, 2004). Rose *et al.* (2005) examined the harpacticoid assemblages at two abyssal, muddy sites in the Angola Basin (from water depths of 5448 m and 5389 m), and found Pseudotachidiidae, Argestidae, Ameiridae, Ectinosomatidae and Neobradyidae as the most dominant of 19 families. Other families also occur in the deep sea although relatively rarely, e.g. Cylindropsyllidae and Paramesochridae traditionally thought to be typically interstitial shallow-water forms apparently have invaded the interstitum lacking muds of the deep sea (Becker *et al.*, 1979; Thistle, 1982; Veit-Köhler, 2005). Por (1969) suggested a pan-bathyal fauna as several genera, such as *Bradya*, *Zosime*, *Malacopsyllus*, *Pseudomesochra* and *Eurycletodes*, are typically reported in deep-sea samples from most oceans. However, as Coull (1972) stated, this has to be checked at the species level, because only few species seem to be widely distributed. It should be mentioned that although many genera (such as *Marsteinia* or *Antarcticobradya*) are deep-sea taxa, i.e. occurring exclusively below 200 m in depth, none of the presently known 52 families is a deep-sea family (Seifried, 2004).

Deep-sea harpacticoid community structure is regulated on small spatial scales (mm to cm) where patch dynamics are a function of biogenic structures (Thistle, 1983b; Thistle & Eckman, 1990b). Several studies have found that the abundances and spatial distributions of certain harpacticoid species are correlated with biologically produced structures like polychaete mudballs

and xenophyophore tests (Thistle, 1982; Levin & Thomas, 1988). Possible mechanisms underlying these associations have been suggested, such as the potential habitat or refuge provided by these structures or a hydrodynamically mediated increase in local food availability (Thistle & Eckman, 1990b). On larger scales, benthic currents and sediment characteristics play a role in regulating community structure. In a physically reworked site, Thistle *et al.* (1999) found lower abundance of surface-dwelling harpacticoids and a higher proportion of interstitial harpacticoids, which could be due to higher exposure at the sediment surface. Also, an increase in the amount of interstitial space by the removal of fine particles could favour interstitial copepods. Shimanaga *et al.* (2004) found that spatial differences in species composition of copepod communities appear to be greater than temporal ones at a deep-sea site in Sagami Bay (Japan, 1430 m depth). However, they suggested the possibility that the reproductive activity of certain copepod species changes seasonally, influenced by detritus input. Differences in reproductive activity between species would consequently result in seasonal changes in the species composition of copepods.

Harpacticoid density

Generally, the abundance of meiofauna in the deep sea seems to be correlated directly with food supply (Thiel, 1983). Food originates mainly from surface water primary production and the amount of food reaching the sea-floor declines with increasing depth, which explains the general tendency for metazoan meiobenthic densities to decrease with increasing bathymetric depth within limited geographical areas (Vincx *et al.*, 1994; Soltwedel, 2000). Meiobenthic standing stock is further affected by a wide range of factors such as oxygen, turbidity, hydrodynamics and sediment heterogeneity (see Heip *et al.*, 1985 for an extended review). For example, Thistle (1988) suggested that a decrease in harpacticoid abundance occurred due to erosion during benthic storms.

Harpacticoid copepods are usually the second most abundant metazoan taxon after nematodes in marine sediments (Hicks & Coull, 1983), and this is also the case in the deep sea (e.g., Tietjen, 1992; Ahnert & Schriever, 2001). Compared to the macrofauna abundance change with depth, harpacticoid abundance decreases less rapidly and therefore they are considered unusually successful in the deep sea (Thistle, 2001). Harpacticoida can constitute between 0% and 36% of the total metazoan meiofauna in the deep sea (e.g. Dinet, 1976: maximum 36% of Harpacticoida) and in the majority of cases they constitute between 5 and 15% (e.g. Tietjen, 1971: 2-15%; Ahnert & Schriever, 2001: 9-12%; Seifried, 2004). Their abundance can range between 0 and 319 individuals per 10 cm^2 (e.g. Shirayama & Kojima, 1994: 319 per 10 cm^2 at 245 m depth). In the Porcupine Seabight, Pfannkuche (1985) reported on average 33 harpacticoids per 10 cm^2 at a depth of 960 m, which is near the sampling depth of the present study. Relative importance and densities of harpacticoids (including nauplii) in the North-East Atlantic region are summarized in Table 2 of Vincx *et al.* (1994).

Harpacticoid diversity

Harpacticoids in the deep sea are characterised by high species diversity and low species dominance (Seifried, 2004). Several hypotheses have been formulated to explain the mechanisms regulating high deep-sea diversity, but they fall under two broad categories: 1) small-scale patch dynamics and 2) large-scale regional processes (for review see Etter & Mulineaux, 2001). Biologically produced structures (such as polychaete mudballs, xenophyophore tests) provide a heterogeneous habitat important for harpacticoid diversity (Thistle, 1979, 1983b; Thistle & Eckman, 1990b; Thistle *et al.*, 1993). Small-scale heterogeneity and thus diversity may also be supported by current-driven resuspension of the seasonally deposited phytodetritus (Rice & Lambshead, 1994). Differences in hydrodynamic stress however were found to be less important for copepod diversity in some regions (Thistle, 1983a). Rose *et al.* (2005) attributed a significant difference in harpacticoid diversity between two abyssal stations to large-scale heterogeneity in food availability. Also, Baguley *et al.* (2006) inferred that processes maintaining harpacticoid diversity in the northern Gulf of Mexico rely on both small-scale dispersal and large-scale food supply mechanisms.

Several authors (Drzycimski, 1969; Hicks & Coull, 1983) reported deep-sea harpacticoid species diversity using the Shannon Wiener index H'. However, Hurlbert's (1971) rarefaction curves are considered more useful in comparing deep-sea studies, because classical diversity indices (as H') are sample-size dependent (Magurran, 1988). Shimanaga *et al.* (2004) summarized rarefaction curves of several bathyal and abyssal harpacticoid studies (figure 2 in Shimanaga *et al.*, 2004), and found the Quagmire site (in the San Diego Trough at 1220 m depth, in Thistle (1978)) as the most diverse deep-sea site, with ES(50) around 32. However, as Shimanaga *et al.* (2004) stressed, comparison is limited as rarefaction assumes that the spatial distribution of each species is homogeneous (Tipper, 1979). Because larger samplers collect more species with heterogeneous distributions, species diversity might be overestimated (Thistle, 1998). Also, difference in the type of sampler used should be considered (cf. Bett *et al.*, 1994).

Baguley *et al.* (2006) proved the typical unimodal relationship between diversity and increasing water depth (e.g., Etter & Mulineaux, 2001; Lambshead *et al.*, 2002) for harpacticoids and found a maximum species diversity (as expressed by expected number of species) at approximately 1200 m water depth, with decreasing diversity moving into deeper waters. However, these unimodal patterns are not universal (Rex *et al.*, 1997; Stuart *et al.*, 2001) and in the western North Atlantic Coull (1972) found a maximum harpacticoid diversity at 3000 m with decreasing diversity thereafter. In the northern Gulf of Mexico, average taxonomic and phylogenetic diversity continue to increase with depth, suggesting greater morphological or functional harpacticoid diversity with increasing depth due to proportionally more higher-order taxa (genera and families) per individual (Baguley *et al.*, 2006).

1.4. HARPACTICOID COPEPODS ASSOCIATED WITH SEAGRASS BEDS AND MACROALGAE

Studies of harpacticoids living as epifauna on a particular substrate (other than sediments) are rare and mostly restricted to the phytal assemblages of seagrasses and macroalgae. Similarly to dead coral fragments which protrude from the seafloor, these macrophytes provide a specific epifaunal habitat as opposed to the infaunal habitat of the surrounding sediment. Knowledge of density, diversity and composition of the associated harpacticoid assemblages, both within the sediment and on the macrophytes, will be summarised to provide information on the structuring factors. In numerous studies of the associated fauna of seagrasses and macro-algae (e.g., Hicks, 1977a,b,c; Hicks & Coull, 1983; Hicks, 1980, 1985; Bell *et al.*, 1988; Bell & Hicks, 1991; De Troch *et al.*, 2001b, 2003; Arroyo *et al.*, 2006), harpacticoid copepods were selected as a key taxon, because of their abundance and habitat specificity as an epiphytic component. Also, the concept of 'isocommunities' (*sensu* Thorson, 1957) wherein often widely separated yet similar substrata are inhabited by the same dominant genera, but with species changing from place to place, is supported by studies of phytal harpacticoids (Hicks, 1985; Hall & Bell, 1993).

Harpacticoid composition

Species composition of the copepod fauna associated with algae, containing low levels of deposited sediments, is usually quite distinct from often closely adjacent sedimentary habitats (Hicks, 1985). Although a significant proportion of sediment-dwelling copepods can enter and disperse through the water column (Walters & Bell, 1986; Walters, 1991), it appears that the effects of emergence on linkages between benthic, pelagic, and phytal habitats are minimal and limited in duration (Walters & Bell, 1994). Harpacticoids with typical 'phytal' habits belong to just a few families and have evolved specific morphological features (such as suction mechanisms, clinging appendages and mucus adhesion) which facilitates purchase on different kinds of algal surfaces (Hicks, 1980, 1985; Hicks & Coull, 1983; Bell *et al.*, 1987). In the phytal, Hicks (1977b) referred to two general sub-associations of harpacticoids, i.e. those characteristic of the sediment trapped by the algae and the true phytal-dwelling forms, which belong to Porcellidiidae, Peltidiidae, Thalestridae, Tisbidae, Tegastidae or Harpacticidae. The accumulated sediment particularly attracts psammic organisms, which are an important component of the meiofauna associated with algae of complex morphology (Moore, 1971; 1972a). Large and morphologically complex macroalgae (such as *Laminaria*) further provide a variety of potential within-plant microhabitats, which are exploited differently by the harpacticoid fauna. The fauna of the fronds strongly differs from the holdfasts in composition and abundance, and mainly consists of few, plant specialist species (Hicks, 1980; Edgar, 1983; Arroyo *et al.*, 2006). Other studies on algae and seagrasses also found that many of the copepods dominating on the fronds were specially adapted to live on flat undulating substrata and cope with mucilagenous secretions produced by frond cells (Hicks & Grahame, 1979; Hicks, 1985; Bell *et al.*, 1987). The harpacticoid fauna of the holdfasts, which retain sediment between the rhizoids, is relatively diverse and is dominated by

taxa also found among sediment and other epibenthic microhabitats (Moore, 1973; Hicks, 1985; Arroyo *et al.*, 2006). Similar patterns of within-plant faunal differences have also been reported for phytal harpacticoids on seagrasses (De Troch *et al.*, 2001b). Also, the growth form and related complexity of the seagrass species seems to influence harpacticoid species composition (De Troch *et al.*, 2001b). The benthic copepod communities in seagrass beds are mainly structured by sediment characteristics and organic matter content, which are related to tidal position and seagrass species (De Troch *et al.* 2003).

Harpacticoid density

There is a general trend of higher meiofauna (Ansari & Parulekar, 1994; Ndaro & Ólafsson, 1999) or copepod densities (Nakamura & Sano, 2005) in sediment of seagrass beds compared to adjacent bare sand areas. Different factors, such as increased food availability (diatoms, detritus) (Klumpp *et al.*, 1989; De Troch *et al.*, 2001a), are thought to influence this pattern. Hicks (1989) even attributed the relative stability of meiofaunal assemblages and absence of significant temporal changes to the unlimited nutritional resources offered by macroalgal coverage. Seagrass beds further stabilise the sediment and reduce detritus resuspension (Terrados & Duarte, 2000). Also, buffering and redirection of currents (depending on seagrass density) can lead to irregular and heterogeneous deposition and accumulation of sediment sizes, promoting habitat heterogeneity (Decho *et al.*, 1985). In unvegetated sandy environments, sediments are frequently resuspended and transported by wave and tidal currents resulting in an unstable environment for many benthic invertebrates (Orth, 1977). However, the opposite trend with higher meiofauna (Aryuthaka & Kikuchi, 1996) or copepod (Decho *et al.*, 1985; Iwasaki, 1999) densities in the bare sediment areas has also been found and attributed to higher predation pressure on meiofauna in seagrass sediments (Decho *et al.*, 1985). Furthermore, mechanical disturbance by the sweeping of seagrass blades has a negative impact on epibenthic meiofauna but not on infaunal species (Hicks, 1989). Nematodes dominate the seagrass sediment (Ndaro & Ólafsson, 1999; De Troch *et al.*, 2001a) which is generally the case in marine sediments (Hicks & Coull, 1983; Hicks, 1985; Heip *et al.*, 1985). The general trend in the phytal habitat is that of a shift to a predominance of harpacticoids and naupliar larvae (Coull *et al.*, 1983; Bell *et al.*, 1984; Hall & Bell, 1993; Arlt, 1995; De Troch *et al.*, 2001a; Arroyo *et al.*, 2004).

Harpacticoid diversity

Different studies indicate that the abundance and species richness of copepods on marine plants can be affected by (1) plant surface area (Hicks, 1980), (2) habitat complexity (Gee & Warwick, 1994; Ólafsson *et al.*, 2001; Jenkins *et al.*, 2002), (3) epiphyte biomass (Hall & Bell, 1993), (4) food availability (Hicks, 1980; Webb, 1990) and (5) plant age (Hicks, 1980; Webb, 1990). Furthermore, plant surface and epiphytic cover are positively related to habitat complexity (Heck & Wetstone, 1977; Hicks, 1980, 1985, 1986). Hicks (1980) stated that an increase in micro-spatial complexity, which is also related to shape, texture, architecture and surface structure of the

plant, allows for significant linearly related increases in harpacticoid species number and diversity. The impact of habitat structural complexity on species composition and diversity is probably the most powerful correlative aspect of macrophyte-meiofauna relations (Hicks, 1985). Greater habitable space, increased nutritional resources and reduced levels of predation or physical disturbance contribute to this relationship. Algae of small, simple fronds offer insufficient protection against predation, desiccation and wave abrasion (Coull *et al.*, 1983; Gibbons, 1988a) and are also inadequate substrata to accumulate both sediment and potential food for meiofaunal organisms (Hicks 1977a, 1980; Edgar, 1990; Gibbons, 1988a, 1988b).

1.5. THE FAMILY LAOPHONTIDAE T. SCOTT, 1905

Taxonomy and systematics

In 1905, T. Scott proposed the family name Laophontidae but did not define the boundaries of the taxon. The Langian scheme (Lang, 1944, 1948) of the Laophontidae comprised 19 genera, which were grouped together with Cletodidae and Ancorabolidae in the superfamily Cletodidimorpha. Por (1986) refuted this grouping and coined the superfamilial name Laophontoidea to accommodate the Laophontidae and Ancorabolidae. Huys (1990) rejected Por's superfamilial definition and re-defined the concept of Laophontoidea T. Scott to include the families Laophontidae T. Scott, Adenopleurellidae Huys, Laophontopsidae Huys & Willems, Orthopsyllidae Huys, and Cristacoxidae Huys on the basis of eight apomorphies. The family Laophontidae was considered the first offshoot in the superfamily and was defined based on the following apomorphies: 1) the presence of a rostrum fused to the cephalosome, 2) the presence of bare antennulary setae, 3) maximum of 3 setae on the mandibular endopod, 4) marginal setation of maxillular arthrite with 7 apical spines, 1 dorsal and 1 ventral seta, and anterior surface without or with only 1 seta (Gómez & Boyko, 2006), 5) shape of basis of P1, 6) migration of inner basal spine/seta of P1 to anterior surface, 7) first endopodal segment of P1 without inner element, 8) reduction of posterior geniculate seta of second endopodal segment of P1 into a tiny seta, 9) anterior geniculate seta of second endopodal segment of P1 modified into large, non-geniculate claw, and 10) the mode of precopulatory mate guarding.

Recently, Huys & Lee (2000) recognised two subfamilies within the Laophontidae and analysed the phylogenetic relationships within the primitive subfamily of Esolinae Huys & Lee, 2000 (now consisting of 8 genera and 20 species), which they considered as relicts of a formerly diverse group. The subfamily Laophontinae T. Scott, 1905 *sensu* Huys & Lee (2000) now consists of 59 genera and comprises 95% of the known laophontid species. It differs from the Esolinae in female P5 morphology, the loss of the outer spine on the distal endopod segment of P2 and additional losses of armature elements on the maxillipedal syncoxa and P1 endopod which were primitively retained in the Esolinae. The relationships between the laophontinid genera however are usually not well understood. The justification for creating new genera has traditionally been based on a purely comparative approach, usually by considering a particular combination of

characters as unique, rather than on phylogenetic grounds. The polyphyletic status of the typegenus *Laophonte* Philippi, 1840, with 44 species the most species-rich genus, is widely accepted and several authors considered the revision of this genus as a conditio sine qua non for a phylogenetic analysis incorporating all genera (Hicks, 1988; Willen, 1996).

Since the publication of the reference list of all known marine harpacticoid copepods by Bodin in 1997, 16 new genera and 37 new species have been described in the Laophontidae. Also, 14 described species were transferred to other genera and one subspecies was raised to the species rank. This high number of new genera and species is an indication that the true diversity of the family is still far from known. Recently, Schizas & Shirley (2006) described a new species of the genus *Apolethon* Wells, 1967 (*Apolethon hippoperus* Schizas & Shirley, 2006), subsequently removed the genus from the Laophontidae and placed it as genus incertae sedis in the superfamily Laophontoidea. In total, the Laophontidae now accommodates 292 valid species and subspecies in 67 genera. In Appendix, a list of all new genera and species including new combinations, since the reference list by Bodin (1997), is provided.

Ecology, morphological plasticity and depth distribution

With nearly 300 species, the cosmopolitan family of Laophontidae is by far the most speciose family within the superfamily Laophontoidea. Especially the subfamily Laophontinae is considered evolutionary highly successful, as displayed by the high species number and variety of habitats explored. The subfamily Esolinae also occurs in a wide variety of habitats despite its low number of known species (20) and, therefore, is considered to be relict of a formerly diverse group (Huys & Lee, 2000). Laophontids are essentially marine, free-living and benthic, and mainly inhabit the intertidal zone or shallow subtidal habitats. They are frequently found among algal assemblages, in which they gain importance especially in the holdfasts of the macrophytes (Dahl, 1948; Moore, 1973; Hicks, 1985; Arroyo *et al.*, 2006). Their prehensile first legs and maxillipeds enables clinging to a particular substrate, such as algal filaments, skeletal elements of invertebrate hosts and other fine microhabitat structures (Hicks, 1980).

One of the most remarkable features of the family is the large variety in body forms. Several authors classified the different body shapes in the Harpacticoida and stressed the relation between body form and mode of existence (Remane, 1952; Noodt, 1971; Hicks & Coull, 1983; Bell *et al.*, 1987). In the Laophontidae, already eight of the nine harpacticoid body shapes, as classified by Coull (1977), can be found and related to different modes of existence. Fiers (1988) demonstrated this diversity of body shapes (Fig. 1) and thoroughly discussed their occurrence throughout the family. The fusiform prehensile body shape of *Laophonte cornuta* Philippi, 1840, the type species of the family, is also the most common one. Interstitial genera are typically vermiform (*Afrolaophonte* and *Klieonychocamptoides*) or cylindrical (e.g. *Laophontina*, *Wellsiphontina*, *Mexicolaophonte*). The depressed body shape of *Platylaophonte* and *Peltidiphonte* enables the animals to live epibenthically on a particular substrate. A compressed body shape permits the members of decapod-associated genera (e.g. *Robustunguis*, *Carcinocaris*) to live between the bristles of their host.

Fusiform, fusiform depressed and fusiform compressed body shapes however are only rarely encountered. This morphological plasticity partly explains the evolutionary success of the Laophontidae. By developing different body shapes, laophontids were able to explore a wide range of habitats and occupy a variety of niches.

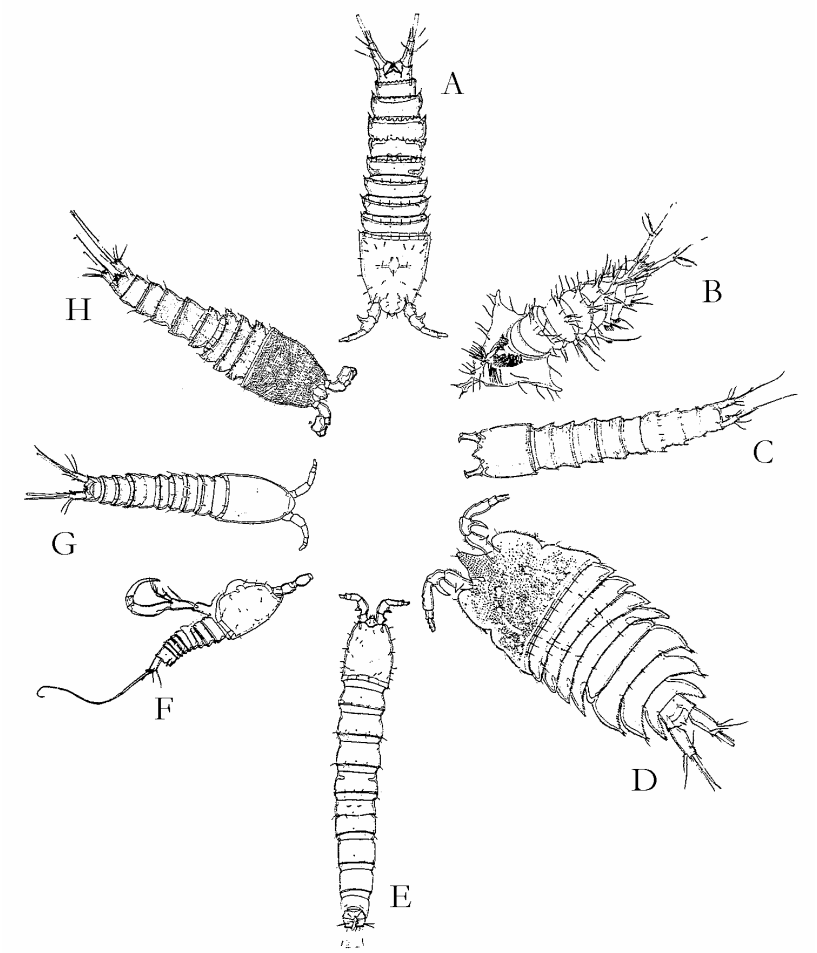


Figure 1. Body shapes in the family Laophontidae (from Fiers, 1988).
(A) fusiform prehensile, (B) fusiform depressed, (C) cylindrical, (D) depressed,
(E) vermiform, (F) compressed, (G) fusiform, (H) fusiform compressed.

The success of Laophontidae in the deep sea is limited as they are only rarely encountered in qualitative or quantitative deep-sea studies (e.g. George & Schminke, 2002). Lee & Huys (1999) reviewed deepwater records of laophontids and regarded the colonization of the deep sea by this family as remarkably unsuccessful. The three exclusively bathyal genera in the subfamily Laophontinae, being *Bathylaophonte* Lee & Huys (in the Atlantic and the Pacific Ocean) and the monospecific *Cornylaophonte* Willen and *Weddellaophonte* Willen (both from the Antarctic deep sea), can be considered as independent colonists of this habitat (Huys & Lee, 2000). Deep sea colonization in the subfamily Esolinae follows a similar erratic trend, with the monotypic genera *Archilaophonte* Willen (Antarctic) and *Bathyesola* Huys & Lee (western Pacific), and a third, secondary deepwater invasion by *Esola profunda* Huys & Lee (Huys & Lee, 2000). Various species

of *Laophonte sensu lato* (such as *L. elongata*, *L. cornuta*, *L. longicauda*), normally encountered at moderate depths, appear to be capable of penetration into the deeper layers of fjords (Lang, 1948; Por 1964b; Drzycimski, 1969). The record of *Bathyesola compacta* Huys & Lee, 1999 at 2765 m depth from the North Fiji Ridge represents the deepest record thus far for the family Laophontidae (Huys & Lee, 2000).

Although certain laophontids are regularly found in salt-marsh and mudflat habitats within river estuaries (Noodt, 1957; Barnett, 1968; Bodin, 1976) or in brackish lagoons (Heip, 1969; Hamond, 1972), tolerance to oligohalinity may have appeared convergently only twice in the family, with the limited success of *Troglophonte* Huys & Lee and a second, cosmopolitan invasion containing the genera *Onychocamptus* Daday and *Folioquinpes* Fiers & Rutledge (Huys & Lee, 2000).

Several lineages also have entered independently into association with other invertebrates. For example, the laophontid genera associated with xanthid crabs (*Coullia* Hamond, 1973; *Robustunguis* Fiers, 1992; *Xanthilaophonte* Fiers, 1991; several species of the *setosa* species group of *Laophonte* Philippi, 1840; probably *Raptolaophonte* Cottarelli & Forniz, 1989; and the recently described *Carcinocaris* Cottarelli, Bruno & Berera, 2006) have similar morphological adaptations (e.g. in habitus shape), which however are considered to be due to convergence rather than reflecting phylogenetic affinity (Fiers, 1992; Cottarelli *et al.*, 2006). Other laophontids have been found as real associates of holothurians (*Namakosiramia* Ho & Perkins), isopods (*Harrietella*) or other decapods (e.g. *Hemilaophonte* Jakubisiak on *Maja squinado*).

1.6. AIMS AND THESIS OUTLINE

The ecology of harpacticoid copepod communities has been investigated in a wide range of habitats in temperate and subtropical seas. In contrast, only limited information is available from the tropics and the deep sea, although their high abundance and diversity suggest harpacticoids play an important role in ecological processes. The physical and biological breakdown of both tropical and cold-water coral skeletons results in a large variety of substrates with different structural complexity, providing a wide range of potential microhabitats for benthic fauna. The main aim of this study was to provide insights in the role of microhabitat type in structuring harpacticoid community composition and diversity. Therefore, different microhabitats were distinguished from degradation products of tropical and cold-water corals, such as coral fragments, coral gravel and coral sand. Meiofauna research has generally focused on infauna of soft-bottoms and mostly neglected the epifauna on hard substrates. Nevertheless, the hard coral substrates investigated in this study might provide a specific epifaunal habitat and it is assumed that the presence of these degradation products influences harpacticoid community structure and diversity. Furthermore, morphological adaptations of associated harpacticoids to these particular substrates were considered for the family Laophontidae.

Coral reefs are known as the most taxonomically diverse of all marine ecosystems, but the nature and extent of this diversity is known only in the broadest outlines for most groups (Paulay, 1996). Both for tropical and cold-water coral reefs, studies have mostly focused on the associated

macro- and megafauna. More recently, associated meiofauna (at higher taxon level) and nematofauna has been investigated by Raes & Vanreusel (2005, 2006) and Raes *et al.* (2007). The present study will focus on composition, diversity and habitat preferences of the second most abundant meiofauna taxon, the order Harpacticoida.

Chapter 2 describes the harpacticoid copepod fauna associated with different coral substrates in a tropical reef lagoon (Zanzibar, Tanzania). The main aim of the study was to investigate the structuring role of microhabitat type. Three microhabitat types were distinguished, namely dead coral fragments, coral gravel and coral sand. Assemblage structure, habitat preferences and biodiversity of the harpacticoid fauna is discussed.

Chapter 3 presents the first characterisation of the harpacticoid copepod fauna associated with deep-water coral substrates (Porcupine Seabight, NE Atlantic). As in the previous chapter, the main aim was to assess the influence of microhabitat type on copepod assemblage structure and diversity. Three different microhabitat types were distinguished, namely dead coral fragments, glass sponge skeletons and the underlying sediment. Composition of the associated harpacticoid fauna is analysed and compared with the typical soft-bottom deep-sea fauna. It is assessed whether the coral degradation zone sustains a specific harpacticoid assemblage and whether hard biogenic substrates provide a specific habitat for 'phytal' taxa.

Qualitative samples from different coral substrates (dead coral fragments, coral gravel, coral sand) along the Kenyan coast yielded numerous representatives of the family Laophontidae, many of which were new to science. This family is considered highly successful in terms of species richness and number of habitats explored. They show a high degree of morphological plasticity and, therefore, are model organisms to study the relation between habitat and morphology. Taxonomy and morphological adaptations to coral substrates within the Laophontidae is investigated in the second part of this study. Only few laophontid species were collected from the deep-sea samples. At present, these new species belong to large (e.g. *Heterolaophonte* Lang, 1944) and polyphyletic (e.g. *Laophonte* Philippi, 1840) genera and, therefore, emphasis is placed on the numerous new Laophontidae from tropical coral substrates.

In **chapter 4**, eight new species of Laophontidae, from different locations in the Indo-West Pacific Ocean, are described and placed in the new genus *Peltidiphonte* gen. n. The affinities to other genera of the family, morphological adaptations to the habitat and biogeography of the genus are discussed. Furthermore, a key to the eight species of the genus is provided. This chapter has been published as *Gheerardyn H., Fiers F., Vincx M., De Troch M., 2006. Peltidiphonte gen. n., a new taxon of Laophontidae (Copepoda: Harpacticoida) from coral substrates of the Indo-West Pacific Ocean. Hydrobiologia 553: 171-199*.

Two new monospecific genera are established in **chapter 5**. Both genera lack sexual dimorphism in the swimming legs. Based on detailed characteristics, they are not closely related to each other. The close relationship of *Propephonte* gen. n., described from the Kenyan coast, with *Peltidiphonte* is discussed. The affinities of *Apistophonte* gen. n., described from the northern coast of Papua New Guinea, are at present difficult to assess. This chapter has been published as

Gheerardyn H., Fiers F., Vincx, M., De Troch, M., 2006. Two new genera of Laophontidae (Copepoda: Harpacticoida) without sexual dimorphism in the endopods of the swimming legs. Zootaxa 1327: 41-62.

Chapter 6 deals with a new species, *Paralaophonte harpagone* sp. n., which is characterised by an extremely specialised maxilliped. This highly specialised structure illustrates that the high degree of morphological plasticity in the family is manifested not only in body shape but also in the appendages. The structure and shape of the maxilliped is analysed throughout the family and a discussion on the possible role of this highly specialised structure is presented. This chapter has been published as *Gheerardyn H., Fiers F., Vincx M., De Troch M., 2006. Paralaophonte harpagone sp. n. (Copepoda: Harpacticoida), a laophontid with an extremely specialised maxilliped. Organisms, Diversity and Evolution 6: Electr. Suppl. 14: 1-9.*

In **chapter 7**, a new monospecific genus, *Spiniferaphonte*, is described from coral gravel. Morphological adaptations to the interstitial habitat and relationships to other genera are discussed. The occurrence of processes on caudal rami and antennules in the family Laophontidae is thoroughly analysed and a hypothesis on the functional role of these processes in interstitial laophontid genera is presented. This chapter has been published as *Gheerardyn H., Fiers F., Vincx M., De Troch M., 2007. Spiniferaphonte, a new genus of Laophontidae (Copepoda, Harpacticoida), with notes on the occurrence of processes on the caudal rami. Journal of Crustacean Biology 27: 309-318.*

Chapter 8 provides a revision of the laophontid genus *Tapholeon* Wells, 1967, with a redescription of the type species. Two new species are described from the Kenyan coast, namely *T. tenuis* sp. n. and *T. inconspicuus* sp. n. Two species, formerly attributed to *Asellopsis* Brady & Robertson, 1873, are allocated to *Tapholeon*, and a redescription of one species is provided. An updated generic diagnosis and a key to the six species of *Tapholeon* are included. Furthermore, the biogeography of the genera *Tapholeon* and *Asellopsis* is discussed. This chapter is currently in press as *Gheerardyn H., Fiers F., Vincx M., De Troch M. Revision of the genus Tapholeon Wells, 1967 (Copepoda, Harpacticoida, Laophontidae). Journal of Natural History.*

In the general discussion and perspectives for future research (**chapter 9**), main patterns in community structure and diversity of harpacticoid copepods associated with tropical and cold-water coral substrates are summarized and a comparison between both studied regions is presented. Morphological adaptations of Laophontidae to coral substrates are discussed, and suggestions for future research are formulated.

Subfamily Esolinae Huys & Lee, 2000

New genera

Genus *Applanola* Huys & Lee, 2000

Applanola hirsuta (Thompson & A. Scott, 1903)

Comb. nov. (Huys & Lee, 2000) for *Laophonte hirsuta* Thompson & A. Scott, 1903

Genus *Archesola* Huys & Lee, 2000

Archesola typhlops (Sars, 1908)

Comb. nov. (Huys & Lee, 2000) for *Laophonte typhlops* Sars, 1908

Archesola longiremis (T. Scott, 1905)

Comb. nov. (Huys & Lee, 2000) for *Laophonte longiremis* T. Scott, 1905

Archesola hamondi Huys & Lee, 2000

Genus *Bathyesola* Huys & Lee, 2000

Bathyesola compacta Huys & Lee, 2000)

Genus *Corbulaseta* Huys & Lee, 2000

Corbulaseta bulligera (Farran, 1913)

Comb. nov. (Huys & Lee, 2000) for *Laophonte bulligera* Farran, 1913

Corbulaseta pacifica Gómez & Boyko, 2006

Corbulaseta tokiokai Gómez & Boyko, 2006

Genus *Troglophonte* Huys & Lee, 2000

Troglophonte spelaea (Chappuis, 1938)

Comb. nov. (Huys & Lee, 2000) for *Laophonte spelaea* Chappuis, 1938

New species

Esola canalis Huys & Lee, 2000

Synonym: *Laophonte bulbifera* Norman, 1911 *sensu* Gurney (1927) (after Huys & Lee, 2000)

Esola galapagoensis Mielke, 1981 grad. nov. (Huys & Lee, 2000)

Esola lobata Huys & Lee, 2000

Synonym: *Esola longicauda* (Edwards, 1891) *sensu* Mielke (1997) (after Huys & Lee, 2000)

Esola profunda Huys & Lee, 2000

Esola vervoorti Huys & Lee, 2000

Synonym: *Esola longicauda* (Edwards, 1891) *sensu* Vervoort (1964) (after Huys & Lee, 2000)

Subfamily Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000

New genera

Genus *Apistophonte* Gheerardyn & Fiers, 2006b

Apistophonte wasiniensis Gheerardyn & Fiers, 2006b

Genus *Bathylaophonte* Lee & Huys, 1999

Bathylaophonte azorica Lee & Huys, 1999

Bathylaophonte faroensis (T. Scott, 1903)

Comb. nov. (Lee & Huys, 1999) for *Laophonte faröensis* T. Scott, 1903

Bathylaophonte pacifica Lee & Huys, 1999

Genus *Carcinocaris* Cottarelli, Bruno & Berera, 2006

Carcinocaris serrichelata Cottarelli, Bruno & Berera, 2006

Genus *Carraroenia* McCormack, 2006

Carraroenia ruthae McCormack, 2006

Genus *Heteronychocamptus* Lee & Huys, 1999

Heteronychocamptus exiguus (Sars, 1905)

Comb. nov. (Lee & Huys, 1999) *Laophonte exigua* Sars, 1905

Heteronychocamptus connexus (Pallares, 1979)

Comb. nov. (Lee & Huys, 1999) for *Paronychocamptus connexus* Pallares, 1979

Genus *Mielkiella* George, 1997

Mielkiella spinulosa George, 1997

Genus *Peltidiphonte* Gheerardyn & Fiers, 2006a

Peltidiphonte andamanica Gheerardyn & Fiers, 2006a

Peltidiphonte cristata Gheerardyn & Fiers, 2006a

Peltidiphonte furcata Gheerardyn & Fiers, 2006a

Peltidiphonte maior Gheerardyn & Fiers, 2006a

Peltidiphonte morovoensis Gheerardyn & Fiers, 2006a

Peltidiphonte ovata Gheerardyn & Fiers, 2006a

Peltidiphonte paracristata Gheerardyn & Fiers, 2006a

Peltidiphonte rostrata Gheerardyn & Fiers, 2006a

Genus *Pontophonte Lee* & Huys, 1999

Pontophonte leuke (Por, 1959)

Comb. nov. (Lee & Huys, 1999) for *Paronychocamptus leuke* Por, 1959

Pontophonte grigae Lee & Huys, 1999

Synonym: *Laophonte brevifurca* Sars, 1920 sensu Griga (1963) (after Lee & Huys, 1999)

Genus *Propephonte* Gheerardyn & Fiers, 2006b

Propephonte duangitensis Gheerardyn & Fiers, 2006b

Genus *Psammoplatypus* Lee & Huys, 1999

Psammoplatypus proprius (Lang, 1965)

Comb. nov. (Lee & Huys, 1999) for *Paronychocamptus proprius* Lang, 1965

Psammoplatypus discipes (Noodt, 1958)

Comb. nov. (Lee & Huys, 1999) for *Klieonychocamptus discipes* Noodt, 1958

Genus *Spiniferaphonte* Gheerardyn & Fiers, 2007

Spiniferaphonte ornata Gheerardyn & Fiers, 2007

New species and new combinations:

Heterolaophonte livingstoni Apostolov & Pandourski, 1999

Laophonte similicornuta Gómez & Boyko, 2006

Loureirophonte minutum Gómez & Boyko, 2006

Loureirophonte psammophila Mielke, 2001

Onychocamptus anomalus (Ranga Reddy, 1984)

Comb. nov. (Lee & Huys, 1999) *Paronychocamptus anomalus* Ranga Reddy, 1984

Onychocamptus fratrisaustralis Gómez, 2001

Paralaophonte harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006c

Phycolaophonte tongariki Gómez & Boyko, 2006

Quinquelaophonte koreana Lee, 2003

Quinquelaophonte prolixasetae Walker-Smith, 2004

Quinquelaophonte quinquespinosa bunakensis Mielke, 1997

Tapholeon arenicolus (Chappuis, 1954)

Comb. nov. (Gheerardyn *et al.* in press) for *Asellopsis arenicola* Chappuis, 1954

Tapholeon chappuissius (Krishnaswamy, 1957)

Comb. nov. (Gheerardyn *et al.* in press) for *Asellopsis chappuissius* Krishnaswamy, 1957

Tapholeon inconspicuus Gheerardyn & Fiers, in press

Tapholeon tenuis Gheerardyn & Fiers, in press

Appendix. New genera and new species, including new combinations, within the family Laophontidae T. Scott, 1905, published after Bodin (1997).

CHAPTER 2

Community structure and microhabitat preferences of harpacticoid copepods in a tropical reef lagoon (Zanzibar, Tanzania)

2.1. ABSTRACT

The community structure, habitat preferences and biodiversity of the harpacticoid copepod fauna associated with different coral substrates in a tropical lagoon (Zanzibar, Tanzania) was investigated. Three microhabitat types were distinguished, namely dead coral fragments, coral gravel and coral sand, which were sampled at two locations (Matemwe and Makunduchi). The harpacticoid fauna appears to be affected by sediment granulometry and by the structural differences between coral and both gravel and sediment. The coral fragments contained a specific assemblage composed of typical 'phytal' taxa (such as *Tisbe*, *Paradactylopodia*, *Dactylopusia*) with an addition of eurytopic and sediment-dwelling forms (*Ameira*, *Ectinosoma*, *Amphiascus*), which could be attracted by the sediment retained between the coral branches. The assemblages of coral gravel and upper sediment layer did not differ significantly from each other with mostly the same dominant genera. The sediment was dominated by the interstitial Paramesochridae at Matemwe and by Tetragonicipitidae at Makunduchi. Especially at Makunduchi, the coral fragments sustained a more diverse assemblage than gravel and the different sediment layers. It was assumed that coral form and complexity, with implications for habitable space, nutritional resources and level of predation, are important in structuring diversity of the associated assemblage.

Keywords: dead coral substrates, harpacticoid copepods, composition, biodiversity, microhabitats, tropical lagoon, Indian Ocean, Zanzibar

2.2. INTRODUCTION

In the backreef lagoon of a fringing reef, the seabed floor is commonly composed of eroded deposits from corals and other carbonate-bearing organisms (Alongi, 1989a). The physical and biological breakdown of the coral skeletons results in a large variety of substrates with different structural complexity, providing a wide range of potential microhabitats for benthic fauna. Despite the considerable research effort on the meiofauna communities associated with carbonate reef sediments (e.g. Alongi, 1989a; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999a; Netto *et al.*, 2003), studies have primarily focused on the associated nematode benthic assemblages and generally ignored the meiofauna living as epifauna on these hard coral substrates. Harpacticoids play an important trophic role in coral sands because of their numerical abundance, capacity to recycle nitrogen and high bacterial ingestion rates (Gray, 1985; Moriarty *et al.*, 1985). Furthermore, they are an important food source for larval, juvenile and small fishes (Hicks & Coull, 1983; Gee, 1989; Coull, 1990; De Troch *et al.*, 1998). However, studies focusing on harpacticoid assemblage structure in the carbonate sands of coral reefs are scarce and geographically restricted, namely at the Bermuda Platform (Coull, 1970; Coull & Herman, 1970), the U.S. Virgin Islands (Hartzband & Hummon, 1974), and Mururoa (Villiers *et al.*, 1987; Villiers, 1988) and Fangataufa Atoll (Villiers & Bodiou, 1996), both in French Polynesia. Generally, sediment granulometry as controlled by reef hydrodynamics was identified as an important

structuring factor of the harpacticoid communities. Studies of harpacticoids living as epifauna on a substrate are rare and mostly restricted to the phytal assemblages of seagrasses and macroalgae (e.g., Hicks & Coull, 1983; Hicks, 1985; Bell *et al.*, 1988; Bell & Hicks, 1991; De Troch *et al.*, 2001b, 2003). These species-rich assemblages are characterised by a specific faunal composition usually quite distinct from often closely adjacent sedimentary habitats (Hicks, 1985). Different within-plant subhabitats may even be occupied by a different suite of species (Hicks, 1977c; De Troch *et al.*, 2001b; Arroyo *et al.*, 2006). Furthermore, the role of habitat structural complexity in determining harpacticoid species number and diversity has been documented (Hicks, 1985; Jenkins *et al.*, 2002).

Up to now, few meiobenthos research has been conducted along the East African coast. Studies have dealt with the associated fauna of seagrass beds, mangroves or the lagoonal soft-bottom in Kenya, Zanzibar and Madagascar (Thomassin *et al.*, 1976; Vanhove *et al.*, 1992; Ólafsson *et al.*, 1995; Ndaro & Ólafsson, 1999; De Troch *et al.*, 2001a; Raes *et al.*, 2007), and mostly emphasized on nematode assemblage structure. Harpacticoid copepod studies have mainly focused on their taxonomy, e.g. in Madagascar (Chappuis, 1954), Réunion (Bozic, 1969), Seychelles (Wells & McKenzie, 1973), Mozambique (Wells, 1967), and Kenya (Fiers & De Troch, 2000; Gheerardyn *et al.*, 2006a, b). Recently, De Troch *et al.* (2001b, 2003) also investigated the composition and structure of harpacticoid communities in Kenyan seagrass beds. The East African coast supports extensive intertidal lagoon flats mainly composed of carbonate sand and in Zanzibar these account for approximately 90% of the total coastal area (Ndaro & Ólafsson, 1999). Along the eastern side of the island, fringing reefs span the coastline and are exposed to strong waves and currents, the principal ocean current affecting Zanzibar Island being the East African Coastal Current (Mbije *et al.*, 2002). Ndaro & Ólafsson (1999) examined the meiobenthos of a shallow lagoon along this coast and found clear nematode assemblages, principally determined by sediment characteristics, in seagrass bed, fine sand and coarse sand habitats. Raes *et al.* (2007) demonstrated the structuring effect of microhabitat type (coral sand, gravel and dead coral fragments) on nematode assemblages along the Kenyan and Zanzibari coasts.

The major aim of this study was to assess the importance of microhabitat type in influencing harpacticoid communities in the lagoon along the east coast of Zanzibar.

2.3. MATERIAL AND METHODS

Sampling and laboratory analysis

Meiofauna samples were collected in the lagoon of the fringing reef, between the reef crest and the sand beach, at two locations along the eastern coast of Zanzibar Island (Tanzania): at Matemwe (MAT), located in the north of the island (5°52' S, 39°21' E; 17/08/2004) and at Makunduchi (MAK), in the south of the island (6°25' S, 39°34' E; 22/08/2004) (Fig. 1). Distance between both locations is 70 km. At each location, three replicates were taken at a distance of five meter from each other, at approximately 400-500 m from the beach. The sampling area

consisted of bare coral sands with patches of coral gravel and dead coral fragments, and was not located adjacent to any seagrass beds, seaweed culture or living coral patches. All material was collected during low tide under a water cover of 0.5 metre. For each replicate, a round, metal core (diameter 30 cm) was placed onto the sediment to delimit the sampling area, in which following microhabitat types were present: coral sand, coral gravel and dead coral fragments (devoid of any algal covering) (Fig. 2). One sediment core (surface area 10 cm^2) for meiofauna was inserted next to the coral fragments and the gravel patch. Then, coral fragments were taken out manually, coral gravel was gently scooped out with a spoon and each of these substrates was put directly in a firm plastic bag. Subsequently, the meiocore was collected and vertically subdivided into three different depth horizons (0-1 cm, 1-3 cm and the remaining sediment), to obtain a more precise view of the harpacticoid sediment assemblage with changing sediment depth. An additional core (surface area 10 cm^2) for granulometric analysis was taken. The dead coral fragments (probably of the genus *Stylophora*) were branched and slightly to more eroded. Although we aimed to sample coral fragments which were similar in structural complexity and morphology, the fragments at Matemwe were generally more eroded, structurally less complex and less protruding from the sediment surface than in Makunduchi. Coral gravel is distinguished from coral sand because small pieces of coral can still be recognised in this microhabitat, whereas this is no longer true for the sediment. In the following, 'coral fragments', 'coral gravel', 'upper', 'middle' and 'lower sediment layer' are abbreviated as 'cor', 'gra', 'sed1', 'sed2' and 'sed3', respectively.

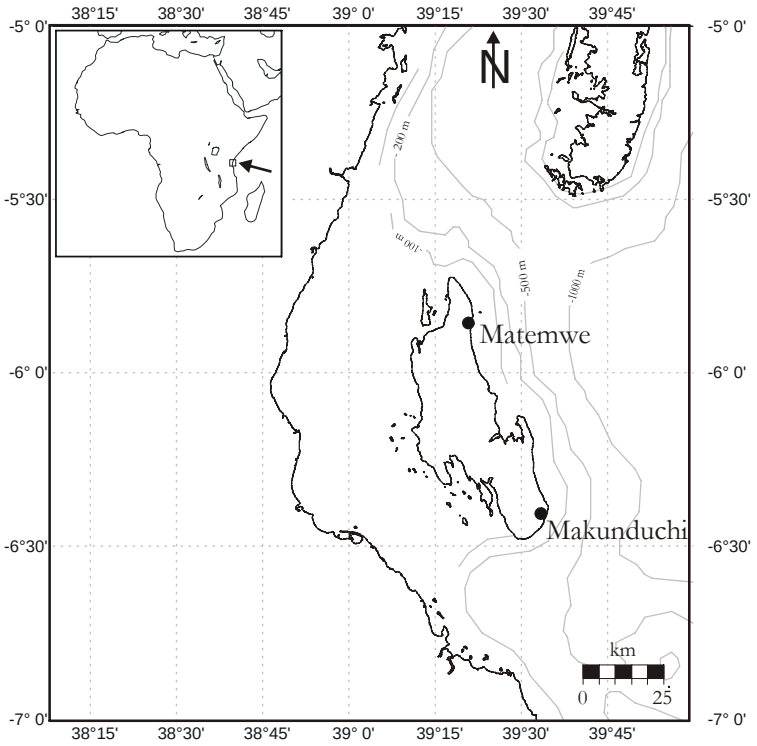


Figure 1. Map of the study area with indication of the sampling sites.
The northernmost island is Pemba, the southernmost Unguja (Zanzibar Island).

After adding $MgCl_2$ to stun the associated fauna, coral fragments and coral gravel were rinsed thoroughly with filtered seawater over a 1 mm and a 32 μm sieve to collect macro- and meiofauna, respectively. Buffered formaldehyde was added to a final concentration of 4%. Meiofauna was extracted from the sediment by density gradient centrifugation, using Ludox HS40 (specific density 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was stained with Rose Bengal. From each sample (coral fragment, gravel and three sediment layers), the first 200 copepods (or all copepods when less than 200 individuals were present) were picked out randomly and mounted in glycerine. All copepods were identified to workingspecies level using Lang (1948, 1965), Boxshall & Halsey (2004) and original descriptions. Assignment of species to genera and families was in accordance with recent literature. The systematic status of Dactylopusiidae Lang, 1936, Pseudotachidiidae Lang, 1936, Rhynchothalestridae Lang, 1948 and Thalestridae Sars, 1905 follows Willen (2000), the status of Miraciidae Dana, 1846 follows Willen (2000, 2002) and the status of Tisbidae Stebbing, 1910 follows Seifried (2003). Furthermore, each harpacticoid species has been designated to one of the nine body shapes as defined by Coull (1977).

Sediment grain size was analysed with a particle size analyser (type Coulter LS100). The characteristics obtained were median grain size, percent silt (<63 μm), percent coarse sand (850-2000 μm), percent gravel (>2000 μm), kurtosis and skewness.

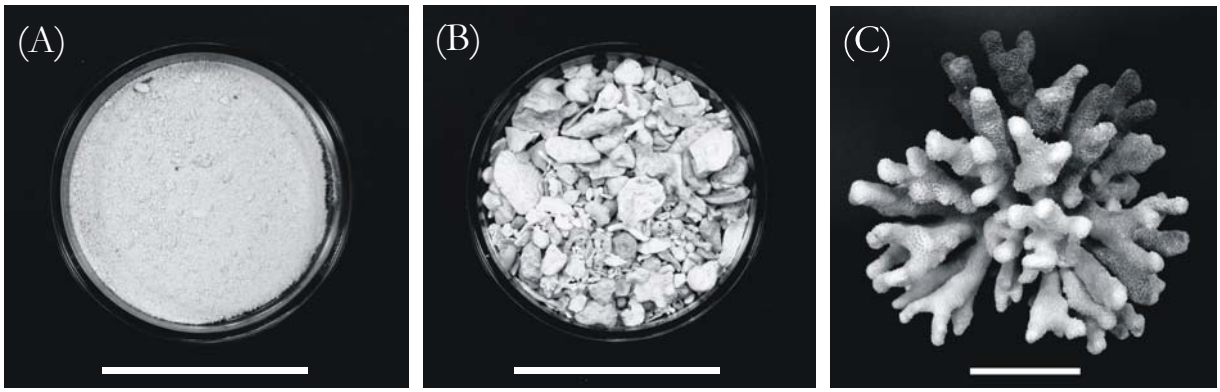


Figure 2. The three microhabitats studied. (A) coral sand, (B) coral gravel, (C) coral fragment (*Porites*/*Stylophora* is given as an example). Scale bars: 5 cm. (From Raes *et al.*, submitted).

Statistical analysis

A non-metric multidimensional scaling two-dimensional plot (MDS) was produced, using the Bray-Curtis similarity index. Due to differences in sample size, data were standardised to relative abundance data and arcsin-transformed prior to analysis. The significance of the MDS (differences in copepod assemblage structure between the different groups) was tested for by two-way crossed ANOSIM. Similarity of percentages (SIMPER) was used to identify the taxa contributing to the differences found in the ordination analysis. All multivariate tests were performed using the PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001).

Several biodiversity indices were calculated. The Shannon Wiener index H' and Pielou's evenness J (Pielou, 1975) were calculated for reasons of comparison with other studies. Hill's diversity numbers (Hill, 1973) gradually change form indices of species richness to indices of dominance with increasing number: N_0 is identical to the number of species, N_1 = exp (H') and N_{inf} reflects evenness. Rarefaction curves were constructed from values of the Expected number of Species (Hurlbert, 1971). The equitability of the copepod fauna was further studied based on the species' abundance distributions as k-dominance curves (Lambshead *et al.*, 1983).

Parametric (ANOVA) analysis of variance was performed on untransformed or log (x+1) transformed data if needed to meet the assumptions for ANOVA. Paired *a posteriori* comparisons were carried out with the Tukey test. For non-parametric data, we employed Kruskal-Wallis ANOVA. Post hoc testing of differences was carried out using pairwise Mann-Whitney U tests. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis. All univariate analyses were performed using the STATISTICA6 software. Indicator species analysis (ISA) was performed using the PC-ORD4 software (McCune & Mefford, 1999). Calculated indicator values were tested for significant values using a Monte Carlo test (Dufrêne & Legendre, 1997). The additive partitioning of species diversity into measures of α- and β-diversity (Veech *et al.*, 2002; Crist *et al.*, 2003) was conducted with PARTITION software.

2.4. RESULTS

In total, 4177 copepods were identified. The bulk of the specimens (79.5%) belonged to the Ordo Harpacticoida, while Cyclopoida made up 20.3% of the individuals. Calanoida were rarely encountered (0.2%, with 9 individuals). Of the 3319 harpacticoid individuals, 55.9% were adults and these were found belonging to 119 species, spread over 60 genera and 23 families. Overall, Paramesochridae (22.2%), Ameiridae (14.9%) and Miraciidae (14.9%) were the dominant families with the latter two having the highest diversity (with 16 and 23 species, respectively) (Table 1). Tisbidae, Ectinosomatidae, Tetragonicipitidae, Dactylopusiidae and Parastenheliidae each constituted between 6% and 8.5%. The other families occurred with less than 5% of relative abundance each. Eight genera (*Ameira*, *Apodopsyllus*, *Kliopsyllus*, *Meiopsyllus*, *Tisbe*, *Diagoniceps*, *Amphiascus* and *Parastenhelia*) occurred with a relative abundance between 5% and 12.5% and together accounted for 56% of the relative abundance. Most genera (37) were poorly represented (each < 1% of relative abundance), while 15 genera were moderately abundant (1%-5% of total abundance). Altogether, 29 species accounted for 80% of the assemblage, with *Ameira* sp. 1, *Kliopsyllus* sp. 1, *Apodopsyllus* sp. 3 and *Diagoniceps* sp. 1 each constituting between 5.2% and 7.4% of relative abundance. Twenty-five species each occurred with a relative abundance between 1% and 5%. The remaining species (90) occurred rarely as each had a relative abundance of less than 1%. A list of identified families, genera and species is provided as Appendix.

Family	%	Number of genera	Number of species
Paramesochridae	22,22	4	10
Ameiridae	14,94	6	16
Miraciidae	14,89	10	23
Tisbidae	8,47	4	8
Ectinosomatidae	7,93	6	13
Tetragonicipitidae	7,39	2	5
Dactylopusiidae	6,36	3	9
Parastenheliidae	6,09	2	3
Laophontidae	4,26	6	11
Harpacticidae	4,15	3	5
Tegastidae	1,02	1	1
Longipediidae	0,59	1	1
Metidae	0,38	1	2
Canthocamptidae	0,32	2	3
Thalestridae	0,27	1	1
Pseudotachidiidae	0,16	1	1
Cletodidae	0,11	1	1
Louriniidae	0,11	1	1
Rhynchothalestridae	0,11	1	1
Ancorabolidae	0,05	1	1
Canuellidae	0,05	1	1
Normanellidae	0,05	1	1
Peltidiidae	0,05	1	1

Tabel 1. Harpacticoid family percentage (%) abundance and number of genera and species in each family identified from the east coast of Zanzibar.

	Matemwe	Makunduchi	1-way ANOVA		Mann-Whitney U
			F-ratio	sign. lev.	
silt (%)	2,8(1,5)	2,2(0,4)	0,254	ns	
median (μm)	408,2(67,9)	440,2(57,6)	0,283	ns	
coarse sand (%)	10,8(2,8)	17,7(1,0)	8,99	*	
gravel (%)	41,2(3,6)	12,4(7,4)			MAT>MAK
Skewness	-2,6(0,5)	-2,2(0,3)	0,536	ns	
Kurtosis	12,1(3,9)	9,9(2,3)	0,432	ns	

Table 2. Mean values and standard deviation (in parentheses) and results of 1-way ANOVA and Mann-Whitney U test evaluating differences in sediment characteristics between both locations. Analyses performed on log (x+1) transformed data. (*): $0.01<p\leq0.05$.

Sediment characteristics

At both locations, the lagoonal soft-sediments are medium to coarse sands with low silt contents (Table 2). Coarse sand percentage was significantly higher at Makunduchi (17.7±1.0 % vs. 10.8±2.8 %), while gravel percentage was significantly higher at Matemwe (41.2±3.6 % vs. 12.7±7.4 %).

Similarity analysis

The MDS ordination indicates that harpacticoid assemblages differ between microhabitats (coral fragments (cor), coral gravel (gra), three depth layers of sediment (sed1, sed2, sed3)) and between locations (Fig. 3). Two sediment samples (from the lowermost sediment layer) appear to be mismatched (at the top and in the lower right corner of the plot), which could be due to their small size (less than 10 individuals each). Although there is a certain degree of overlap, a clear trend of different copepod composition appears across the different microhabitats. Samples are slightly more separated according to location (averaged over all microhabitat groups), as confirmed by the two-way crossed ANOSIM (global R=0.379, p=0.001 between microhabitats; global R=0.485, p=0.001 between locations). Pairwise tests (Table 3) indicated highly significant differences between coral samples and each of the other microhabitats (gra, sed1, sed2, sed3) with respect to their faunal composition. Gravel samples were not significantly different from samples of the upper sediment layer. However, they were significantly (but not clearly) different from the middle and lower layers. Among sediment layers, there was a significant difference between the upper and lowermost layers. Samples from the middle and lower sediment layers each formed rather scattered clusters, indicating high variability among replicates.

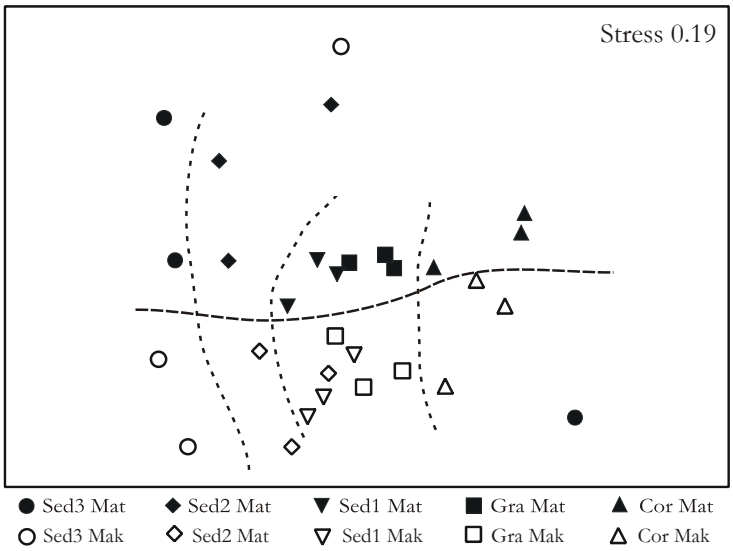


Figure 3. Multidimensional Scaling (MDS) two-dimensional ordination plot of all samples. Stress value is indicated. The dashed line separates samples from the different locations, the dotted line separates the different microhabitats (except samples from gravel and upper sediment layer).

	Coral fragments	Coral gravel	Upper layer	Middle layer	Lower layer
Coral fragments		**	**	**	*
Coral gravel	0,778		NS	*	*
Upper layer	0,889	0,185		NS	*
Middle layer	0,852	0,296	0,093		NS
Lower layer	0,565	0,389	0,306	-0,074	

Table 3. Results of ANOSIM pairwise tests: values of the R-statistic and corresponding p-levels are indicated. (**): $0.001<p\leq0.01$; (*): $0.01<p\leq0.05$; (NS): not significant.

MDS ordinations at the genus and the family level (not shown) produced the same pattern of a changing composition across the different microhabitats and a slightly clearer separation between locations, as indicated by two-way crossed ANOSIM. Also, pairwise tests indicated significant differences for the same combinations, except that at the genus level there is also a significant (but not clear) difference between gravel samples and the upper sediment layer (with R=0.296, p=0.05).

Average similarity among samples in terms of community composition (as indicated by SIMPER) is highest for gravel (52.8%) at Matemwe, and highest for the upper sediment layer (48.3%) at Makunduchi. At both locations, average dissimilarity between microhabitats is lowest between gravel and upper sediment layer (56.9% and 55% at MAT and MAK, respectively). Coral samples from both locations are slightly more comparable to each other (dissimilarity value: 64.7%), than they are to the other microhabitats within their respective location (dissimilarity cor-gra at MAT: 66.5%, all other values higher than 75%).

Characterisation of the harpacticoid assemblages

Both locations share four of their five most dominant families on coral fragments, namely Dactylopusiidae, Ectinosomatidae, Tisbidae and Ameiridae (Fig. 4). At both locations, these families, together with Laophontidae and Miraciidae, explained over 90% of similarity among the coral samples and generally were important in explaining dissimilarity between coral and any other microhabitat (SIMPER). At Makunduchi, the typically phytal family Tegastidae explained between 9.5% and 6.7% of the dissimilarity with every other microhabitat (SIMPER). At the family level, a significant habitat preference as indicated by ISA was only provided for Dactylopusiidae and Ectinosomatidae for coral at Makunduchi (IV=80.1, p=0.013 and IV=46.0, p=0.012, respectively). In the gravel samples, Ameiridae, Parastenheliidae, Tisbidae (at both locations), Harpacticidae (at Matemwe) and Miraciidae (at Makunduchi) are the dominant families, which agree well with those from the upper sediment layer (being Ameiridae, Miraciidae and Parastenheliidae at both locations). At Makunduchi, average relative abundance of Parastenheliidae was significantly higher in gravel and upper sediment layer than on coral (Mann-Whitney U tests, p=0.049). Furthermore, Paramesochridae (with 20.8% of relative abundance) at Matemwe and Tetragonicipitidae (with 9.8%) at Makunduchi also predominate in the upper sediment layer. At Matemwe, middle and lower sediment layers are strongly dominated by Paramesochridae (with 74.4% and 86.6%, respectively). At Makunduchi, the middle layer is codominated by Tetragonicipitidae, Miraciidae and Ameiridae, while the lower one is dominated by a single family, Tetragonicipitidae (with 67.9%). It is clear that especially in middle and lower sediment layer faunal composition differs distinctly between both locations.

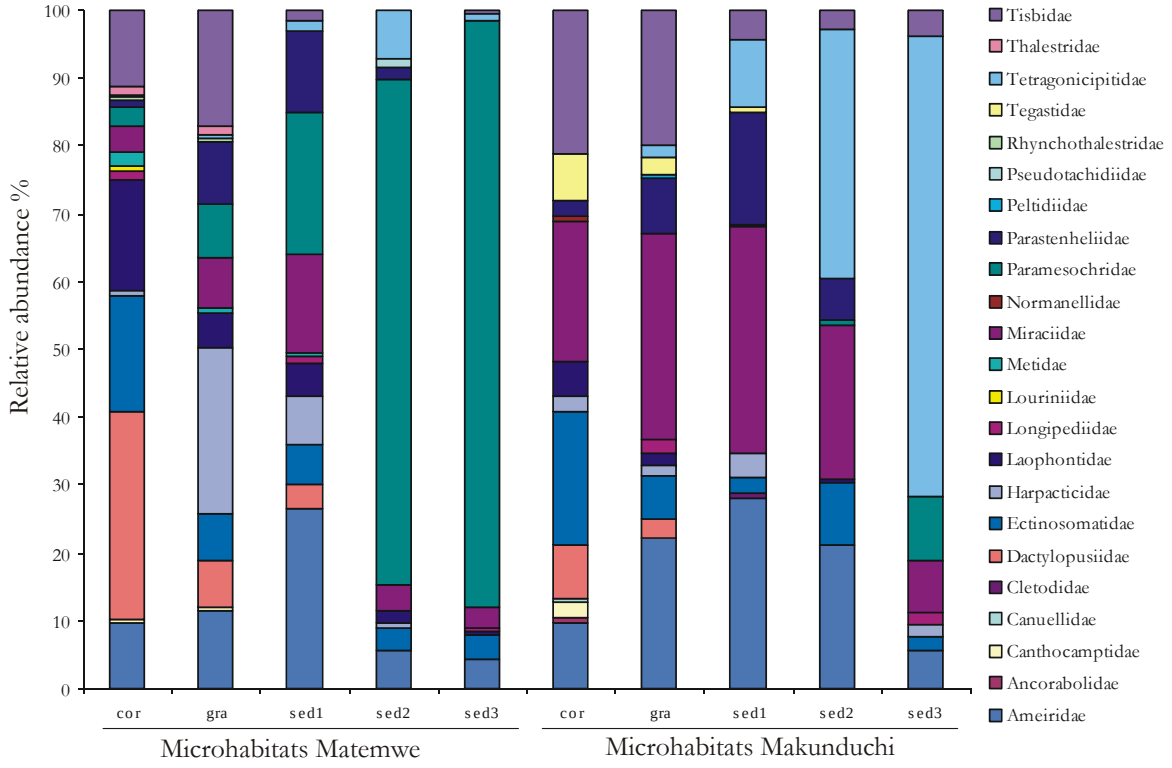


Figure 4. Harpacticoid family composition per microhabitat at Matemwe and at Makunduchi, based on pooled samples per microhabitat (with cor: coral; gra: gravel; sed1: upper, sed2: middle and sed3: lower sediment layer).

An overview of the most abundant genera in each of the microhabitats from both locations is given in Table 4. Per location, all genera with a relative abundance >2% in at least one microhabitat (calculated over all samples per microhabitat, per location) are represented. At both locations, genera as *Dactylopusia*, *Ectinosoma*, *Tisbe* and *Paradactylopodia* (at Matemwe) predominate on the coral fragments. More clearly at Makunduchi, dominant genera in gravel and upper sediment layer are the same, namely *Paramphiascopsis*, *Parastenhelia* and *Robertgurneya*. Both locations differ in dominant genera in upper and particularly middle and lower sediment layers, with mainly paramesochrid genera at Matemwe, and *Diagoniceps* (Tetragonicipitidae) at Makunduchi. All genera exhibiting significant indicator values (as indicated by ISA) are listed in Table 5. Only one genus showed a significant preference for gravel, namely *Zausodes* (at Matemwe). At both locations, the genera *Dactylopusia* and *Ectinosoma* showed a significant preference for coral.

	Matemwe						Makunduchi				
	cor	gra	sed1	sed2	sed3		cor	gra	sed1	sed2	sed3
Ameira	9,7	10,3	25,0	5,3	3,5	*Ameira*	9,2	16,4	24,0	9,9	3,8
Amphiascus	0,8	2,9	2,1	0,9	1,0	*Amphiascus*	12,1	13,0	9,3	7,7	
Apodopsyllus				23,8	49,5	*Apodopsyllus*				0,7	7,5
Dactylopusia	12,8	1,1	2,1			*Bulbamphiascus*	3,4	0,5	4,0	5,6	1,9
Diagoniceps		0,6	1,6	6,6	1,0	*Dactylopusia*	6,9	2,4			
Ectinosoma	16,3	4,0	1,6	0,9		*Diagoniceps*			0,9	28,9	60,4
Halectinosoma	0,4	0,6	2,1			*Ectinosoma*	13,8	2,4		4,9	
Hastigerella		2,3	2,1	2,2	3,0	*Halectinosoma*	1,7	3,4	2,2	2,8	
Heterolaophonte	3,9					*Mesochra*	2,3				
Karllangia		5,1	3,6	1,3		*Nitokra*		5,8	2,2	8,5	1,9
Kliopsyllus	2,7	8,0	13,0	22,5	13,9	*Paralaophonte*	4,6	1,0			
Laophonte	2,7	1,1				*Paramphiascopsis*	0,6	10,1	13,8	1,4	1,9
Meiopsyllus			7,8	28,2	22,8	*Parastenhelia*	2,3	7,7	16,4	6,3	
Paradactylopodia	17,9	5,7	1,0			*Phyllopodopsyllus*		1,9	8,9	7,7	7,5
Paralaophonte	8,9	4,0	0,5		0,5	*Psyllocamptus*	0,6		1,3	2,1	
Parastenhelia	1,2	4,0	8,3	0,4		*Robertgurneya*	0,6	5,3	6,2	4,9	1,9
Robertgurneya	0,8	4,0	11,5	2,2	1,5	*Robertsonia*	2,3				
Scutellidium	1,9	2,3				*Scutellidium*	3,4	0,5	0,4	0,7	1,9
Stenhelia (D.)	2,3				0,5	*Tegastes*	6,9	2,4	0,9		
Tapholeon			3,6	1,8		*Tisbe*	13,8	19,3	0,9	0,7	1,9
Tisbe	8,9	14,9	1,6		0,5	*Tisbella*	2,3		3,1	1,4	
Zausodes	0,8	24,6	7,3	0,9		*Zausodes*		1,4	3,6		1,9

Table 4. Dominant harpacticoid genera in each microhabitat, per location. Genera with a relative abundance >2% in at least one microhabitat (per location) are given.

Genus	Preferred Microhabitat	Indicator Value	sign. lev.
Matemwe			
Dactylopusia	coral	81,5	**
Paradactylopodia	coral	73	*
Ectinosoma	coral	70,2	**
Laophonte	coral	72	*
Zausodes	gravel	62,7	*
Makunduchi			
Dactylopusia	coral	80,4	*
Ectinosoma	coral	64,4	*
Paralaophonte	coral	84,5	*

Table 5. Indicator genera within each location, as specified by an indicator species analysis (ISA). Only taxa with a significant habitat preference are listed. Indicator values, preferred microhabitat and significance levels are provided. (***): $p \leq 0.001$; (**): $0.001 < p \leq 0.01$; (*): $0.01 < p \leq 0.05$.

Over the complete dataset, the dominant body shapes (as defined by Coull, 1977) are fusiform prehensile (48.4% of the individuals) and vermiform (23.5%). Copepods with fusiform depressed, fusiform compressed and fusiform shape occur with a relative abundance between 6.7% and 7.7%. The four remaining habitus shapes (depressed, fusiform not prehensile, compressed and cylindrical) are only rarely encountered (less than 4% of relative abundance each). Copepods of fusiform prehensile body shape were dominant in coral, gravel and upper sediment layer at both locations (ranging between 33.1% and 87.6% of relative abundance), and also in middle and lower sediment layer at Makunduchi, due to the presence of Ameiridae, Miraciidae and Tetragonicipitidae (Fig. 5). Vermiform copepods were especially dominant in middle and lower sediment layer at Matemwe (over 75% of relative abundance) and increased in relative importance with increasing sediment depth. The relative importance of fusiform depressed copepods was higher on coral and gravel than in the sediment layers, and this was proven statistically significant at Matemwe (Kruskal-Wallis ANOVA and Mann Whitney U tests, $p < 0.05$). Also, fusiform compressed copepods were significantly more important on coral than in any sediment layer at Matemwe (Kruskal-Wallis ANOVA and Mann Whitney U tests, $p < 0.05$). At Makunduchi, average relative abundance of fusiform copepods (comprising all ectinosomatid genera except *Hastigerella*) was significantly higher on coral than in any other microhabitat (Kruskal-Wallis ANOVA and Mann Whitney U tests, $p < 0.05$). Depressed copepods mostly occurred in gravel and upper sediment layer at Matemwe.

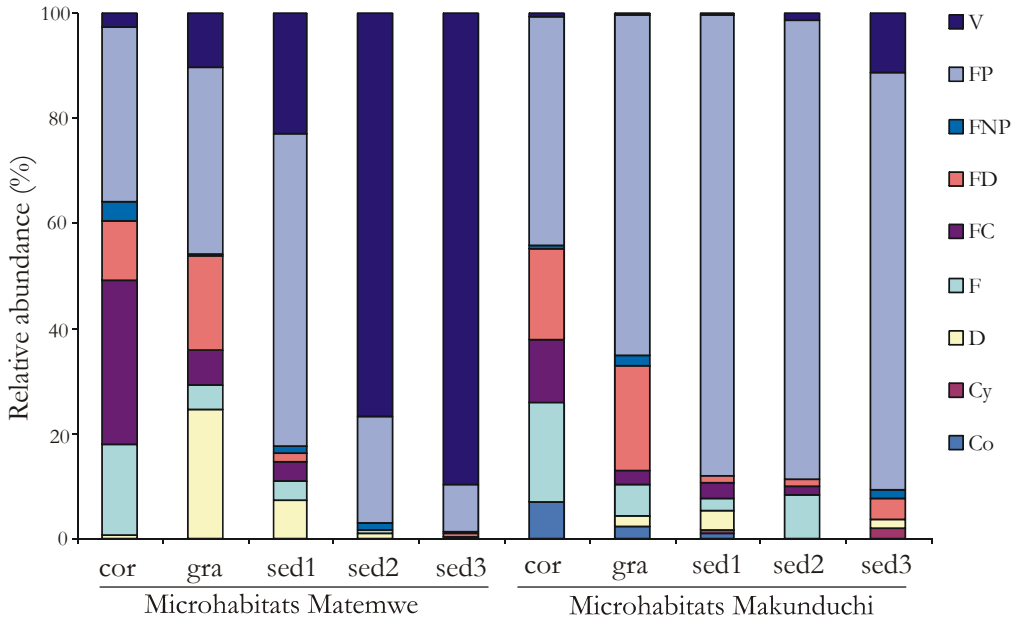


Figure 5. Composition of body shapes for each microhabitat, per location. Body shapes as defned by Coull (1977), with V: vermiform, FP: fusiform prehensile, FNP: fusiform non-prehensile, FD: fusiform depressed, FC: fusiform compressed, F: fusiform, D: depressed, Cy: cylindrical and Co: compressed.

Biodiversity

There was a significant difference in copepod diversity among microhabitats (Table 6 and 7), as expressed by indices of species richness (H', N_0, N_1). However, trends were different between locations. At Matemwe, coral, gravel and upper sediment layer did not differ significantly from each other, but were more diverse than middle and lower sediment layer as shown by H' and N_1. For the Shannon-Wiener index H', diversity was significantly higher in coral, gravel, upper sediment layer than in the lower sediment layer, and higher for coral than middle sediment layer. At Makunduchi however, coral was significantly more diverse than any other microhabitat, as shown by N_1. Evenness was generally high and there were no significant differences between microhabitats, as expressed by J. At both locations, N_{inf} is significantly higher on coral and indicates low dominance on coral.

		Matemwe					**Makunduchi**				
		cor	gra	sed1	sed2	sed3	cor	gra	sed1	sed2	sed3
N_0	Avg	23,67	20,67	19,00	12,00	8,67	27,33	17,00	14,33	16,00	7,33
	sd	5,19	4,03	3,74	5,89	2,05	6,13	5,72	1,89	2,16	4,50
H'(log_2)	avg	3,95	3,75	3,71	2,69	2,37	4,39	3,19	3,04	3,33	1,91
	sd	0,38	0,19	0,20	0,59	0,10	0,36	0,33	0,24	0,46	0,74
N_1	Avg	16,02	13,53	13,20	6,98	5,20	21,66	9,35	8,32	10,56	4,26
	sd	4,49	1,74	1,89	2,60	0,38	5,01	2,14	1,47	2,95	2,07
N_{inf}	Avg	6,32	4,58	5,40	3,45	2,60	8,29	2,99	3,35	4,59	3,47
	sd	1,05	0,77	0,92	0,70	0,66	1,69	0,44	0,41	2,02	2,51
J'	Avg	0,87	0,86	0,88	0,83	0,79	0,93	0,80	0,79	0,84	0,84
	sd	0,03	0,02	0,04	0,09	0,13	0,02	0,02	0,03	0,11	0,23
ES(50)	Avg	18,58	20,38	17,91	13,28		26,85	14,18	12,39		
	sd	3,97	0,67	2,41	3,78		1,32	2,26	1,35		

Table 6. Biodiversity indices: Hill's diversity numbers N_0, N_1, N_{inf}, the expected number of species ES (50), the Shannon-Wiener diversity index H' and Pielou's evenness J. The average (Avg) value with standard deviation (sd) is given per microhabitat, per location.

	one-way ANOVA			Kruskal-Wallis
	F-ratio	sig. lev.	Post hoc.	sig. lev.
Matemwe				
N_0	4,1	*	cor>sed3	
J'	0,5	NS		
H'(log_2)	8,8	**	cor>sed2,sed3; gra,sed1>sed3	
N_1	6,4	**	cor>sed2,sed3	
N_{inf}	6,4	**	cor>sed2,sed3; sed1>sed3	
Makunduchi				
N_0	5,2	*	cor>sed3	
J'				NS
H'(log_2)	7,4	**	cor>sed3	
N_1	9,4	**	cor>gra,sed1,sed2,sed3	
N_{inf}				cor>gra,sed1

Table 7. Results of 1-way ANOVA and Kruskal-Wallis tests for harpacticoid diversity indices between the different microhabitats, per location. (**): $0.001<p\leq0.01$; (*): $0.01<p\leq0.05$; (NS): not significant.

Overall, similar trends were found with K-dominance curves and rarefaction curves based on pooled samples per microhabitat (cor, gra, sed1, sed2, sed3), per location. At Matemwe, the fauna of coral, gravel and upper sediment layer is characterised by an even distribution which is comparably high in each of these microhabitats (Fig. 6A). Middle (sed2) and lower (sed3) sediment layer show a less even distribution, especially in the lowest sediment layer where the dominant species (*Apodopsyllus* sp. 3) attains a relative abundance of 33.7%. At Makunduchi, there is a separation with the coral sustaining the most even distribution (Fig. 6B). The curves of gravel, upper and middle sediment layer are not separable and show a slightly higher dominance than in the coral samples. In the lowest sediment layer, the dominant species (*Diagoniceps* sp. 1) attains a relative abundance of 60.4%. Rarefaction curves of the pooled samples per microhabitat show that at Matemwe species diversity in coral, gravel and upper sediment layer is similar and higher than middle and lower sediment layer (Fig. 7A). The lowermost layer sustains the lowest diversity. At Makunduchi (Fig. 7B), coral shows the highest diversity, which is distinctly higher than the diversity of coral at Matemwe (ES(100) = 41.5 at Makunduchi, ES(100) = 30.4 at Matemwe). Further, the middle sediment layer is more diverse than gravel and upper sediment layer (which has the lowest diversity). No trends can be determined on the diversity of the lowest sediment layer, as these samples yielded few individuals.

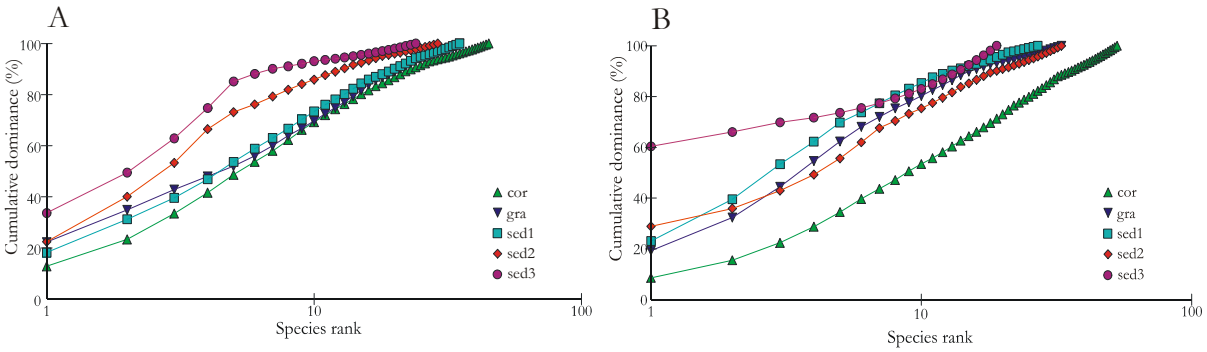


Figure 6. K-dominance curves of pooled samples per microhabitat (cor, gra, sed1, sed2, sed3), (A) at Matemwe and (B) at Makunduchi.

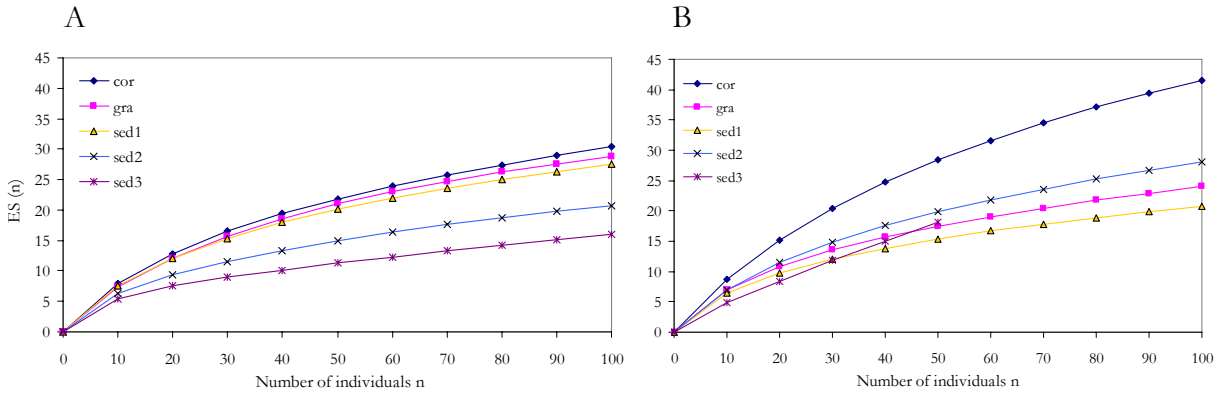


Figure 7. Rarefaction curves of pooled samples per microhabitat (cor, gra, sed1, sed2, sed3), (A) at Matemwe and (B) at Makunduchi.

In figures 6 and 7, sediment layers were treated separately to obtain a more precise view of the change in diversity with increasing sediment depth. When sediment layers are pooled, sediment in Matemwe shows a slightly lower evenness than coral and is barely separable from gravel, as shown by K-dominance curves (Fig. 8A). At Makunduchi, there still is a clear separation with the coral sustaining the most even distribution (Fig. 8B). The curves of sediment and gravel are barely separable and show a higher dominance than the coral samples. Both at Matemwe and Makunduchi, the entire community combined over all microhabitat types (pooled) shows a more even distribution than sediment. Rarefaction curves (with all sediment layers pooled) produced similar results. At Matemwe, species diversity in sediment is slightly lower than gravel and coral (Fig. 9A). At Makunduchi, coral shows the highest diversity and is higher than sediment and gravel, which are barely different from each other (Fig. 9B). At both locations, the diversity of the entire community combined over all microhabitat types (pooled data) is higher than diversity of the sediment. In this combined community, it is not possible to calculate the relative importance of each of the three microhabitats and, therefore, it should not be interpreted as a representation of the natural situation.

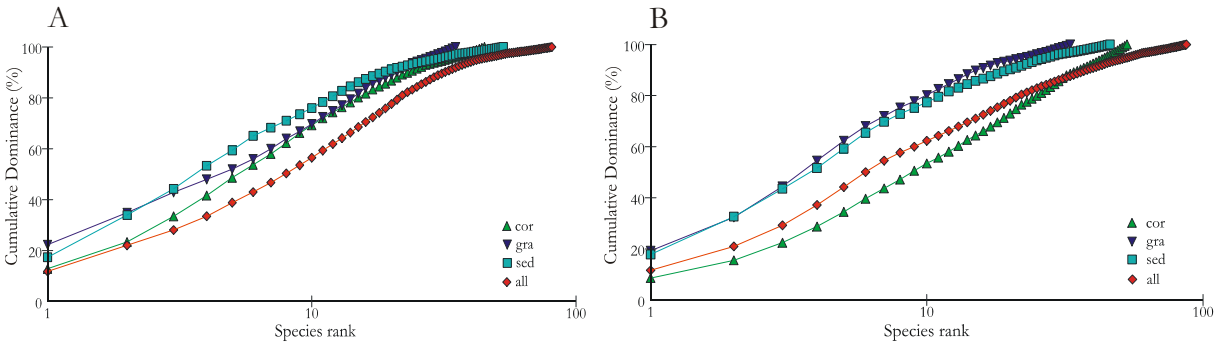


Figure 8. K-dominance curves of pooled samples per microhabitat (cor, gra, sed) and for the combined community over all microhabitats (all), (A) at Matemwe and (B) at Makunduchi.

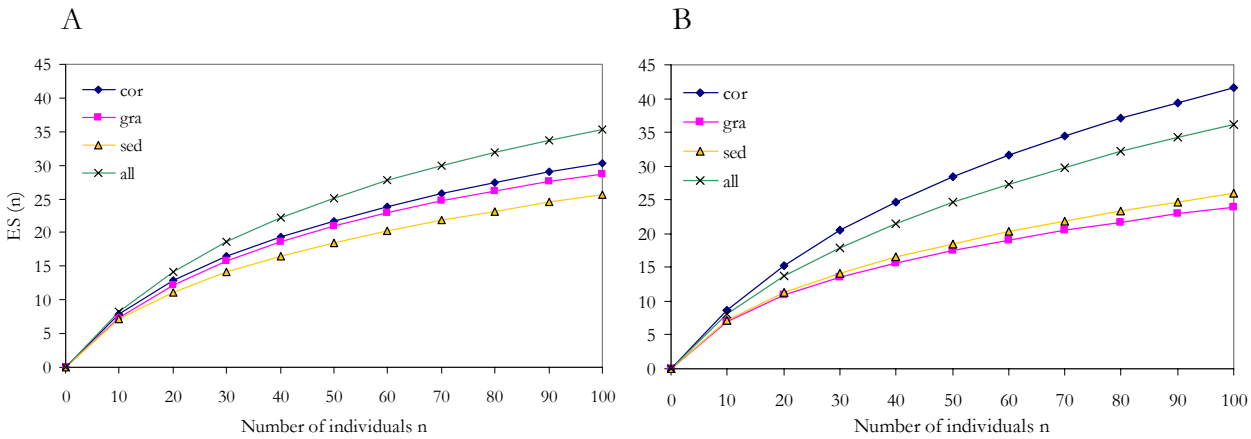


Figure 9. Rarefaction curves of pooled samples per microhabitat (cor, gra, sed) and for the combined community over all microhabitats (all), (A) at Matemwe and (B) at Makunduchi.

Additive partitioning of diversity (Fig. 10) indicates that total species richness (γ) is mainly attributed to differences between microhabitats (β_1, 41.4%). Average diversity within microhabitats (α) and β-diversity due to turnover between locations (β_2) contribute 28.8% and 29.8%, respectively. In contrast, 71% of the Shannon index is explained by α diversity within microhabitats, while β_1-diversity and β_2-diversity contribute less (19.4% and 9.1%, respectively).

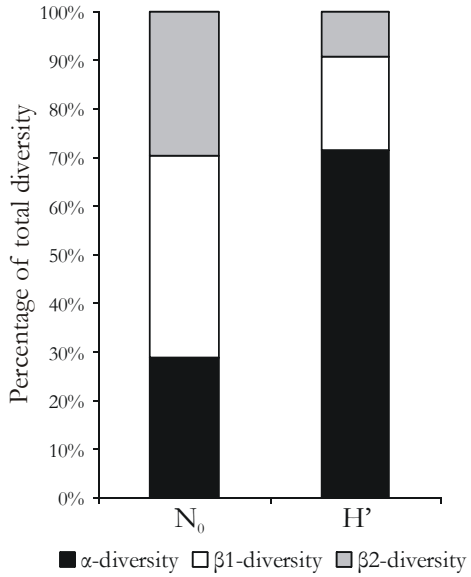


Figure 10. Additive partitioning of total diversity for the number of species N_0 and for Shannon-Wiener diversity H'. β_1-diversity is the fraction of β-diversity resulting from differences in microhabitat. β_2-diversity is the fraction of β-diversity resulting from differences between locations.

The sediment alone yielded 69 species spread over 41 genera and 15 families. The eight families exclusively present on coral and/or gravel constituted less than 0.5% of the total assemblage each. Also, the 19 genera added by the coral and gravel samples were relatively rare, with *Heterolaophonte* (on coral) and *Laophonte* (on coral and gravel) the most important (with 0.5% and 0.6% of the total assemblage, respectively). The genera restricted to sediment, coral or gravel occurred only sporadically, generally with less 0.3% of relative abundance (of the total assemblage). Thirteen of 42 genera occurring in coral samples are restricted to this microhabitat. Only 3 genera (each found with one individual) of the 32 genera in the gravel samples were restricted to gravel. Twelve (of 41) genera were restricted to sediment, with *Tapholeon* (with 0.6% of relative abundance), *Apodopsyllus* (with 8.6%) and *Meiopsyllus* (with 6.7%) the most important.

By adding coral and gravel samples, an additional 50 species were found of which *Paradactylopodia* sp. 3 (occurring on coral and gravel) was the most abundant (with 1.9% of the total abundance). Species restricted to one of the microhabitats (35 of 71 species in coral, 7 of 51 in gravel, 26 of 69 in sediment) were rare (each constituting less than 1% of the total assemblage), with the exception of *Apodopsyllus* sp. 2 and sp. 3 (with 2.1% and 5.8%, respectively) and *Meiopsyllus* sp. 2 and sp. 3 (with 3.5% and 3.0%, respectively).

2.5. DISCUSSION

The results of this study indicate that dead coral fragments, coral gravel and the different layers of the nearby coral sand differ in composition and diversity of the harpacticoid fauna that they harbour. At both locations, there is a trend of changing copepod composition across these microhabitats. Multivariate analysis showed that the composition of the coral assemblage is significantly different from that in gravel and every sediment layer. The copepod fauna of the gravel samples did not differ significantly from the upper sediment layer, and differed only slightly (but significantly) from middle and lower sediment layers. Further, fauna composition changed with increasing sediment depth.

The harpacticoid fauna associated with the coral fragments was mainly composed of genera typically found in phytal assemblages, such as *Tisbe*, *Paradactylopodia*, *Dactylopusia* (synonymous with *Dactylopodia*) and *Tegastes* (at Makunduchi) (Hicks, 1985), with an addition of genera often found among sediment and other epibenthic microhabitats, such as *Ameira*, *Ectinosoma*, *Amphiascus* and *Paralaophonte* (Hicks & Coull, 1983). Although some species of certain genera (such as *Ectinosoma*) are not easily classified and occur in a wide range of habitats, it is not unlikely that sediment-bound forms are attracted by the sediment retained between the coral branches. The meiofauna (including harpacticoids) associated with the holdfasts of macroalgae is not strictly phytal, but a mixture of inhabitants from phytal, epibenthic and interstitial habitats, associated mainly with the sediment retained between the holdfast structure and the variety of niches and refuge provided by them (Moore, 1972a; Moore, 1973; Hicks, 1977b; Arroyo *et al.*, 2004, 2006). Similarly, the sediment trapped by the coral fragments might provide a habitat for sediment-dwellers, while the complex microtopography of the coral branches might be a suitable substratum for true epibenthic or even 'phytal' harpacticoids. The rough surface of the coral skeleton could particularly favour copepods with strongly prehensile maxillipeds and first legs for efficient clinging, but is unsuitable for taxa such as Porcellidiidae and Peltidiidae. These families have dorso-ventrally flattened bodies and adapted mouthparts to facilitate adhesion to the smooth, flat thalloid surface of algae (Noodt, 1971; Hicks, 1980, 1985). Klumpp *et al.* (1988) and Preston & Doherty (1994) examined the crustacean cryptofauna associated with dead coral substrata and reported Thalestridae and Peltidiidae as important harpacticoid families. In those studies, coral fragments were colonised by filamentous algae and other epiphytes which might explain the presence of a typical phytal family such as Peltidiidae.

Multivariate analysis proved gravel not significantly different from the upper sediment layer. Especially at Makunduchi, these microhabitats share mostly the same dominant genera (such as *Paramphiascopsis*, *Parastenhelia*, *Robertgurneya*), with coral gravel also containing genera dominant on coral (e.g. *Tisbe*, *Paradactylopodia*) or in sediment (*Kliopsyllus*). Only one genus showed a significant preference for gravel, namely *Zausodes* (at Matemwe), which by its depressed habitus most likely has an epibenthic lifestyle. The changing copepod composition across the different microhabitats of coral, gravel and upper sediment layer as indicated by ordination mainly has to be attributed to

differences in contributions of the taxa that are present. The coral assemblage is not composed of unique, specific families or genera restricted to this microhabitat, as is often found in assemblages on algae or hard substrates (containing low levels of deposited sediments) which are distinct or even largely nonoverlapping from often closely adjacent sedimentary habitats (Hicks, 1985; Atilla *et al.*, 2003). Species restricted to one of the microhabitats occurred only sporadically, with the exception of representatives of *Apodopsyllus* and *Meiopsyllus* in the sediment. However, although dissimilarity between coral samples of both locations is rather high (64.7%), this value is consistently lower than dissimilarity between coral and every other microhabitat within each location. This indicates that coral assemblages from both locations are slightly more comparable to each other in terms of faunal composition than they are to gravel and sediment layers within their respective location.

The sediment assemblages from both locations differ distinctly in composition, especially in middle and lower sediment layers by the occurrence of paramesochrid genera (*Meiopsyllus*, *Kliopsyllus* and *Apodopsyllus*) at Matemwe and of Tetragonicipitidae (especially *Diagoniceps*) at Makunduchi. The granulometric analysis revealed that the coarse sand fraction was significantly more important at Makunduchi, which explains the occurrence of Tetragonicipitidae, generally a conspicuous member of coarse shell-gravel assemblages (Hicks & Coull, 1983). Paramesochridae then are typically known as interstitial inhabitants of fine to medium sands. Several studies of carbonate reef-associated sediments also identified sediment granulometry as controlled by reef hydrodynamics (with its effect on other parameters of the environment) as an important structuring factor of the associated harpacticoid (Coull, 1970; Villiers & Bodiou, 1996) and nematode communities (Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999a; de Jesús-Navarrete, 2003). The finer sediment of Matemwe particularly favours harpacticoids with vermiform and rather small body shapes (Paramesochridae and *Hastigerella*), which, together with their reduced swimming legs, are adapted to move through narrow spaces between the sand grains. Evidently, the interstitial spaces in the coarser sand at Makunduchi are larger and this explains the pronounced occurrence of harpacticoids with fusiform prehensile body shape (mainly Ameiridae, Miraciidae and Tetragonicipitidae). These harpacticoids are generally larger and have more well developed swimming legs, due to which they can move through the systems of spaces between the larger sediment particles. Copepods with fusiform depressed and fusiform compressed body shapes, evidencing an epibenthic or phytal life style (Noodt, 1971; Coull, 1977), were more important in the coral and gravel samples.

The harpacticoid fauna associated with the different microhabitats investigated in this study appears to be affected by the structural differences between coral and both gravel and sediment, and by changes in sediment grain size. Not only the nature of the substrate, but also the conditions encountered in these particular microhabitats (e.g. with respect to hydrodynamical stress and food availability) could be important structuring factors. In a comparable study of the associated nematode assemblages of coral sand, coral gravel and coral fragments, Raes *et al.*

(2007) also found that microhabitat type is a major structuring factor. They concluded that nematode communities are even more affected by changes in sediment grain size than by the structural differences between sediment and coral fragments. The coral fragments were considered preferable habitats particularly for nematodes able to withstand the current's eroding effect, such as the epifaunal Epsilonematidae and Draconematidae. Also, current activity can erode detritus from the coral fragments which would explain the low abundance of non-selective deposit feeding nematodes Raes *et al.* (2007).

Despite a similar change in harpacticoid composition across microhabitats at both locations, the trends in species diversity were different. At Makunduchi, coral fragments sustained a more diverse assemblage (both in terms of species richness and evenness) than gravel and the different sediment layers, whereas at Matemwe, coral was not significantly different from gravel and upper sediment layer. Coral skeletons at Makunduchi were generally less eroded and structurally more complex than at Matemwe. When sediment layers were pooled, total diversity of the sediment (both in terms of species richness and evenness) was slightly lower than gravel and coral at Matemwe. At Makunduchi, total sediment diversity was lower than coral and not distinctly different from gravel.

For phytal assemblages, several studies indicated that an increase in habitat complexity allows for a linear increase in harpacticoid species number and diversity (Hicks, 1980; Gee & Warwick, 1994; Ólafsson *et al.*, 2001; Jenkins *et al.*, 2002). Greater habitable space, increased nutritional resources and reduced levels of predation contribute to this relationship. Although we did not quantify the differences in corallum morphology, we assume that the observed differences in complexity might be responsible for dissimilar trends in diversity. Several studies on macrocrustacean cryptofauna have demonstrated that spatial separation of the (living) coral branches influences the variation in species abundance and faunal composition (Lewis & Snelgrove 1990; Vytopil & Willis 2001). Vytopil & Willis (2001) found greater abundance and species richness of macro-epifauna on tightly branched coral species in comparison to their rarity or absence on open-branched species and related this to the higher protection afforded by the more complex habitat structure. Similarly, the level of structural complexity provided by certain coral fragments might be high enough for the associated meiofauna to provide refuge against predation. Furthermore, coral form may have important implications for the associated epifauna, including increased potential for niche separation (Begon *et al.*, 1990) and modification of the local hydrodynamical environment (Helmuth *et al.*, 1997) with implications for the nutritional resources available. Regarding two typically epifaunal nematode families, Raes *et al.* (submitted) found higher diversity on the coral fragments and attributed this to the adaptations of these families to live in an exposed habitat. However, they warned the higher diversity might also be caused by the more considerable differences in community structure between coral samples, resulting in a higher total number of species.

Oxygen tension and food supply are important factors in determining the vertical distribution of meiofauna within the sediment. Harpacticoids are typically the meiobenthic taxon most sensitive to a decrease in oxygen (Hicks & Coull, 1983), which might explain the clear decrease in species diversity and evenness with increasing sediment depth at Matemwe. Dissolved oxygen might penetrate to deeper layers in the coarser sand of Makunduchi and be responsible for the high diversity of the middle sediment layer.

The analysis of additive partitioning of diversity shows that β-diversity related to differences between microhabitats is the most important in contributing to total species richness. Also, β-diversity related to difference in location is rather high. When taking abundance data into account, most of the diversity is explained by average sample diversity (α), which means that the same 'common' species occur across the different microhabitats and locations. The sediment samples alone yielded 69 species spread over 41 genera and 15 families. By adding coral and gravel samples, an additional 50 species, 19 genera and 8 families were found. Although the addition of microhabitats and locations contributes significantly to total species richness, these added species are generally rare.

In conclusion, microhabitat type is important in structuring the associated harpacticoid assemblages. The coral fragments support a specific assemblage composed of epibenthic or phytal taxa with an addition of sediment-dwelling species attracted by the sediment retained between the branches. Furthermore, there are trends in diversity of the associated harpacticoids of the different microhabitats. The observed differences in growth form and complexity of the coral fragments, with implications for habitable space, nutritional resources and level of predation might be important in structuring diversity of the associated assemblage.

Ameiridae Monard 1927 (part.), Lang 1936

Ameira Boeck 1865 (9 sp.)

Nitokra Boeck 1865 (3 sp.)

Praeleptomesochra Lang 1965 (1 sp.)

Psyllocamptus T. Scott 1899 (1 sp.)

Stenocopia Sars 1907 (1 sp.)

Ameirinae gen. 1 (1 sp.)

Ancorabolidae Sars 1909, Lang 1944, Lang 1948

Laophontodes T. Scott 1894 (1 sp.)

Canthocamptidae Sars 1906 (part.), Monard 1927 (part.), Lang 1948

Mesochra Boeck 1865 (2 sp.)

Canthocamptidae gen. 1 (1 sp.)

Canuellidae Lang 1944

Brianola Monard 1926 (1 sp.)

Cletodidae T. Scott 1905 (part.) *sensu* Por 1986

Enhydrosomella Monard 1935 (1 sp.)

Dactylopusiidae Lang 1936

Dactylopusia Norman 1903 (5 sp.)

Paradactylopodia Lang 1944 (3 sp.)

Dactylopusiidae gen. 1 (1 sp.)

Ectinosomatidae Sars 1903 (part.), Olofsson 1917

Ectinosoma Boeck 1865 (5 sp.)

Halectinosoma Lang 1944 (2 sp.)

Halophytophilus Brian 1917 (1 sp.)

Hastigerella Nicholls 1935 (1 sp.)

Pseudobradya Sars 1904 (1 sp.)

Sigmatidium Giesbrecht 1881 (3 sp.)

Harpacticidae Sars 1904

Harpacticus Milne-Edwards 1840 (1 sp.)

Perissocope Brady 1910 (2 sp.)

Zausodes C.B. Wilson 1932 (2 sp.)

Laophontidae T. Scott 1905

Esola longicauda Edwards 1891

Heterolaophonte Lang 1944 (1 sp.)

Laophonte cornuta Philippi 1840

Laophonte ciliata Noodt 1964

Laophonte inornata A. Scott 1902

Paralaophonte Lang 1944 (3 sp.)

Paralaophonte congenera (Sars 1908)

Tapholeon tenuis Gheerardyn & Fiers *in press*

Laophontinae gen. 1 (1 sp.)

Longipediidae Sars 1903 (part.) *sensu* Lang 1948

Longipedia Claus 1863 (1 sp.)

Louriniidae Monard 1927

Lourinia Wilson 1924 (1 sp.)

Metidae Sars 1910

Metis Philippi 1843 (2 sp.)

Miraciidae Dana 1846

Amphiascoides Nicholls 1941 (2 sp.)

Amphiascus Sars 1905 (8 sp.)

Bulbamphiascus Lang 1944 (1 sp.)

Haloschizopera Lang 1944 (1 sp.)

Paramphiascella Lang 1944 (1 sp.)

Paramphiascopsis Lang 1944 (1 sp.)

Robertgurneya Lang 1944 (4 sp.)

Robertsonia Brady 1880 (1 sp.)

Stenhelia (Delavalia) Boeck 1865 (3 sp.)

Typhlamphiascus Lang 1944 (1 sp.)

Normanellidae Lang 1944 *sensu* Huys & Willems 1989

Normanella Brady 1880 (1 sp.)

Paramesochridae Lang 1944

Apodopsyllus Kunz 1962 (4 sp.)

Kliopsyllus Kunz 1962 (1 sp.)

Kliopsyllus furcavaricatus (Kunz 1974)

Meiopsyllus Cottarelli & Forniz 1994 (3 sp.)

Scottopsyllus Kunz 1962 (1 sp.)

Parastenheliidae Lang 1944

Karllangia Noodt 1964 (1 sp.)

Parastenhelia Thompson & A. Scott 1903 (2 sp.)

Peltidiidae Sars 1904

Peltidium Philippi 1839 (1 sp.)

Pseudotachidiidae Lang 1936

Sentiropsis Huys & Gee 1996 (1 sp.)

Rhynchothalestridae Lang 1948

Rhynchothalestridae gen.1 (1 sp.)

Tegastidae Sars 1904

Tegastes Norman 1903 (1 sp.)

Tetragonicipitidae Lang 1944

Diagoniceps Willey 1930 (1 sp.)

Phyllopodopsyllus T. Scott 1906 (4 sp.)

Thalestridae Sars, 1905 *sensu* Lang 1948

Eudactylopus A. Scott 1909 (1 sp.)

Tisbidae Stebbing 1910, Lang 1944 1948

Scutellidium Claus 1866 (2 sp.)

Tisbe Lilljeborg 1853 (3 sp.)

Tisbella Gurney 1927 (2 sp.)

Tisbidae gen. 1 (1 sp.)

Appendix. List of identified families and genera (with number of morphospecies between parentheses) from the eastern coast of Zanzibar.

CHAPTER 3

Biodiversity of harpacticoid copepods in the Porcupine Seabight (North-East Atlantic)

3.1. ABSTRACT

The harpacticoid copepod fauna associated with cold-water coral substrates was investigated in the Porcupine Seabight (North-East Atlantic). The main aim was to assess the influence of microhabitat type on copepod assemblage structure. Therefore, different substrate types were distinguished, namely dead coral fragments, glass sponge skeletons and the underlying sediment. Although nature and structure of the examined microhabitats are different and the associated faunas most likely experience different conditions (e.g. in terms of food supply and physical disturbance), it appears that coral fragments and underlying sediment do not harbour distinctly different copepod assemblages, apart from some subtle differences. Several factors might be important in explaining this pattern. The sediment retained between the branches of the coral fragments might provide a habitat for typical sediment-dwellers which obscure the presence of real epibenthic taxa. Also, active migration by swimming and the close contact between upper sediment layer and overlying biogenic substrates may facilitate considerable exchange between the microhabitats. At the family level, the copepod fauna in the Porcupine Seabight does not seem to differ markedly from other deep-sea studies in which essentially the same families are dominant. However, at the genus and species level it is apparent that the hard biogenic substrates provide a habitat suitable for typical 'phytal' taxa, with prehensile first legs and modified body shapes. Substantial information from neighbouring soft-bottom and coral-free regions is necessary to assess whether regional diversity is increased by the presence of these complex habitat-providing substrates. Coral fragments and sediment were both characterised by high species diversity and low species dominance, and did not differ markedly in this. This might indicate that copepod diversity is not substantially influenced by hydrodynamical stress, which however was the main structuring factor of the associated nematode assemblages.

Keywords: cold-water coral, harpacticoid copepods, composition, diversity, microhabitat, NE Atlantic, Porcupine Seabight

3.2. INTRODUCTION

Cold-water corals occur in the upper part of the bathyal zone throughout the world, with *Lophelia pertusa* (Linnaeus, 1758) being recorded from the continental shelf of the NE Atlantic more frequently than from any other place in the world (Rogers, 1999; Freiwald, 1998, 2002; Freiwald *et al.*, 2002; De Mol, 2002). The diversity of *L. pertusa* coral reefs seems to be of a similar order of magnitude to that of some shallow-water tropical coral reefs (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Rogers, 1999), which is reflected both in terms of overall diversity and for diversity within certain taxonomic groups (Rogers, 1999). High habitat complexity, intermediate productivity (food supply), the relatively stable environment and the highly diverse fauna of the continental slope are among the factors which explain that these reefs can support a diverse community (Rogers, 1999). Moreover, dead stony corals have been observed to provide a substrate for an associated fauna even more diverse than in living colonies (Jensen & Frederiksen,

1992; Mortensen *et al.*, 1995; Freiwald, 2002). Recently, Raes & Vanreusel (2005, 2006) presented the first study of the associated metazoan meiofauna and nematofauna of a cold-water coral degradation zone in the Porcupine Seabight (North-East Atlantic Ocean), and concluded that the dead *L. pertusa* framework and associated substrates enables more taxa to be present and particularly favours harpacticoid copepods, naupliar larvae and polychaetes. Preceding studies dealing with epifauna on either living or dead *L. pertusa* had focused on the macro- and megafauna (Jensen & Frederiksen, 1992; Mortensen *et al.*, 1995; Fosså & Mortensen, 1998; Rogers, 1999). It is clear that the complex matrix of living and dead branches of *Lophelia* increases the spatial heterogeneity of the seabed.

Although harpacticoid copepods are the second most abundant metazoans in the deep sea (e.g. Tietjen, 1992; Ahnert & Schriever, 2001), studies on their diversity and species composition are scarce and mostly restricted to analyses at higher taxonomic level. Sofar, no complete diversity analysis has been made of north-eastern Atlantic deep-sea copepod communities (Vincx *et al.*, 1994). Systematic and careful studies are, however, indispensable in order to analyse the spatial patterns in species composition of deep-sea communities on regional and global scales (Shimanaga *et al.*, 2004).

This is the first study investigating the harpacticoid copepod fauna associated with cold-water coral substrates. In particular, we examine the importance of different microhabitats (i.e. dead coral fragments of *L. pertusa*, skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886 and underlying sediment) in structuring harpacticoid species composition and diversity. For the associated nematofauna, Raes & Vanreusel (2006) found that the large biogenic substrates provide a microhabitat for rare, epifaunal taxa and that fragments of both substrata within the sediment increase habitat complexity and hence biodiversity. Furthermore, we assess whether the coral degradation zone harbours a typical harpacticoid community.

3.3. MATERIAL AND METHODS

Study area

The Porcupine Seabight is a large, amphitheatre-shaped embayment in the continental margin to the southwest of Ireland. It is bounded to the west by the Porcupine Bank, to the east by the Irish Shelf and to the southeast by the Goban Spur. Along the eastern margin of the basin partly buried and seabed coral banks represent the Belgica Mound Province, with many of the banks hosting living deep-water corals (mainly the framework builder *L. pertusa*) and associated fauna (Henriet *et al.*, 1998; De Mol *et al.*, 2002). These cold-water corals are present only on the basinward flank of the mounds (De Mol *et al.*, 2002). The upper slope (<1000 m) settings are subject to a complex hydrodynamic regime with interactions of tidal currents, vertical mixing, northward flow along the north-eastern continental slopes, internal tides and the effect of topography (De Mol, 2002). Furthermore, smaller features (such as coral banks and local irregularities in the topography) influence the local hydrodynamic and sedimentary regime.

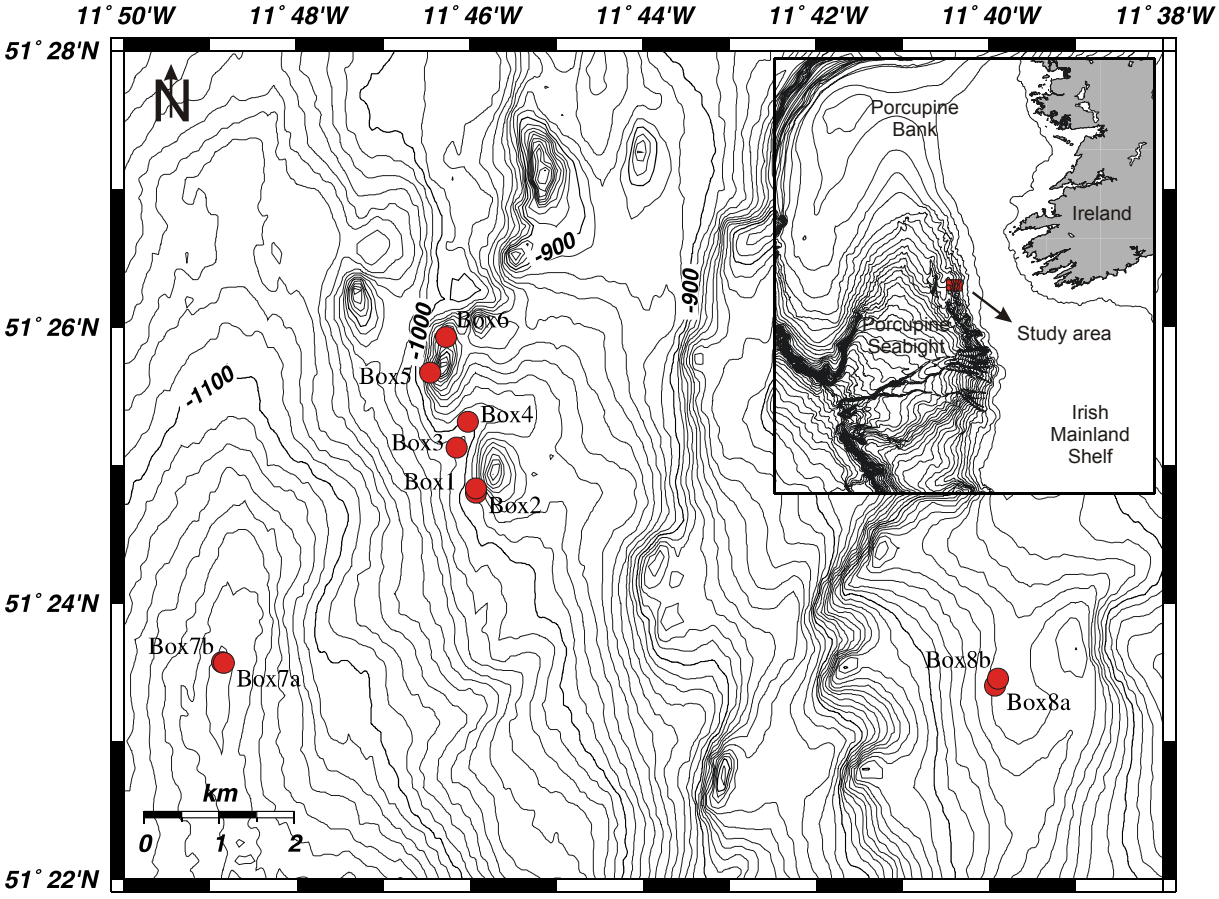


Figure 1. Map of the Porcupine Seabight (NE Atlantic Ocean), and a detail showing the ridge of mounds in the Belgica Mound Province, with indication of the exact boxcore locations. Multibeam bathymetry by courtesy of AWI Bremerhaven, contour interval at 10m.

Boxcore	Date	Coordinates		Depth (m)	Sample	Harpacticoid density
		Latitude	Longitude			
Box1	17.06.2000	51°24.802'N	11°45.924'W	1005	sed1	19 ± 7
					cor1	250
					spo1	-
Box2	17.06.2000	51°24.824'N	11°45.932'W	1000	sed2	4 ± 3
					cor2	272
Box3	07.05.2001	51°25.1290'N	11°46.1553'W	972	sed3	26
					cor3	97
					spo3	207
Box4	07.05.2001	51°25.3120'N	11°46.0226'W	969	sed4	9
					cor4	665
Box5	07.05.2001	51°25.6700'N	11°46.4553'W	950	sed5	4
					cor5	129
Box6	07.05.2001	51°25.9290'N	11°46.2717'W	880	sed6	27
					cor6	208
Box7a	25.05.2003	51°23.572'N	11°48.859'W	1168	sed7a	6 ± 2
Box7b	25.05.2003	51°23.567'N	11°48.843'W	1175	sed7b	3 ± 1
Box8a	25.05.2003	51°23.403'N	11°39.936'W	649	sed8a	2 ± 0.5
Box8a	25.05.2003	51°23.454'N	11°39.901'W	646	sed8b	12 ± 2

Table 1. Depth, date, geographical position, and microhabitats sampled per boxcore taken at the Porcupine Seabight, with harpacticoid density (as individuals/10 cm² ± SD for sediment samples and individuals/100ml for coral and sponge samples). (sed = underlying sediment, cor = coral fragment, spo = sponge skeleton).

Sampling site and procedure

In the Porcupine Seabight, eight locations were sampled with a round box corer (Netherlands Institute for Sea Research, diameter 32 cm) from the RV Belgica (Table 1). Six locations were situated in the coral degradation zone and yielded 6 sediment, 6 coral and 2 sponge samples. The other two locations each yielded 2 samples of coral-free sediments.

The material from the coral degradation zone (CDZ) originates from two seabed mounds in the Belgica Mound Province at depths between 880 and 1005 m (Fig. 1), with boxes 3 and 4 taken between the two mounds and boxes 1, 2, 5 and 6 taken from the seamound flank. In each case, the surface of the sediment was partly or entirely covered with several dead fragments of the cold-water coral *L. pertusa* and skeletons of the glass sponge *A. bocagei*. After collecting the coral fragments and sponge skeletons separately, three cores (surface area 10 cm^2) for collection of meiofauna were pushed into the underlying sediment. Consequently, three microhabitat types are defined in our samples from the coral degradation zone: (1) coral fragments, (2) sponge skeletons (i.e. the two large biogenic substrates) and (3) the underlying sediment (Fig. 2). It was observed that the underlying sediment contained small fragments of both biogenic substrates, as well as some small mollusc shells and echinoid radiolas. Only box 1 and 3 supplied an additional sample of a sponge skeleton. During sampling of boxcores 3 to 6, the three sedimentcores per boxcore were erroneously collected together. Boxes 1, 2 and 3 were named box IV (2000), box V (2000) and box IV (2001) in a previous study on the associated nematofauna by Raes & Vanreusel (2006). To be able to compare the copepod fauna from the coral degradation zone with that from coral-free sediments, two boxcores were taken to the west of the mounds in the Arwen Channel (box 7a and 7b) and two boxcores to the east of the mounds (box 8a and 8b). Again three sediment cores (10 cm^2) were collected per boxcore and were vertically subdivided into layers of 1 cm. Copepods were collected from the upper three centimeter (0-1, 1-2 and 2-3 cm). All material was fixed with 4% buffered formaldehyde. In each boxcore an additional core (10 cm^2) was inserted for granulometry analysis.

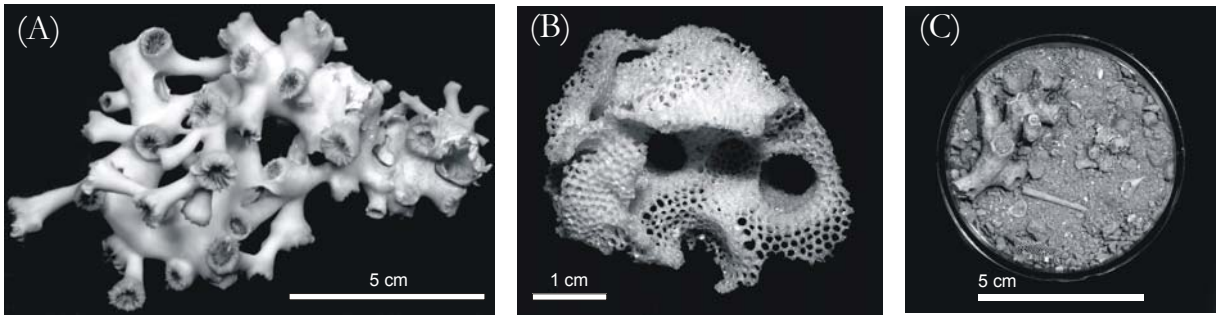


Figure 2. An overview of the three microhabitat types. (A) dead *Lophelia pertusa* fragment; (B) dead *Aphrocallistes bocagei*-skeleton; and (C) underlying sediment, which contains small coral and sponge debris, echinoid radiolas, and small bivalve and gastropod shells. (From Raes & Vanreusel, 2005).

In the laboratory, each coral or sponge sample was rinsed thoroughly over a 1 mm and 32 μm sieve to collect macrofauna and meiofauna, respectively. Volumes of all examined biogenic substrates were measured by immersion, as a proxy for surface area. Meiofauna from the sediment was extracted by density gradient centrifugation, using Ludox HS40 (specific density 1.18) as a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Per sample, the first 200 randomly encountered copepods (or all copepods when less than 200 were present) were picked out and mounted in glycerine. All copepods were identified to species using Lang (1948, 1965), Huys *et al.* (1996), Boxshall & Halsey (2004) and original species descriptions. Assignment of species to genera and families was in accordance with recent literature. The systematic status of Pseudotachidiidae Lang, 1936 and Rhynchothalestridae Lang, 1948 follows Willen (2000), the status of Miraciidae Dana, 1846 follows Willen (2000, 2002), and the status of Idyanthidae Lang, 1944, Neobradyidae Olofsson, 1917, and Zosimidae Seifried, 2003 follows Seifried (2003).

Statistical analysis

The non-parametric procedures multidimensional scaling two-dimensional plot (MDS) and analysis of similarity (ANOSIM) were used to compare sample similarity based on species composition (Clarke & Gorley, 2001). Per boxcore, copepods from the three sedimentcores were pooled and treated as one sediment sample. Prior to analysis, all species (72) present as singletons were removed from the species-level dataset. Similarly, all genera (27) and families (2) present as singletons were removed from their respective dataset. Due to differences in sample size, the data were standardised to relative abundance data. Analyses were performed at family, genus and species level. At each level, MDS ordinations were made on the complete dataset, all samples from the CDZ and the samples from the CDZ without sed2 and sed5 (because their representativeness is rather limited as they constitute of less than 10 individuals each). MDS was produced based on Bray-Curtis similarities between samples, calculated using the PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001). The stress value gives a measure for goodness-of-fit of the MDS ordination: a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). One-way Analysis of similarities (ANOSIM) was performed to test for significant differences in copepod community structure between the different microhabitats. Indicator species, genus and family analysis was performed using the PC-ORD4 software, in analogy with the indicator species analysis (ISA) of Dufrêne & Legendre (1997). Calculated indicator values were tested for significant values using a Monte Carlo test.

Diversity consists of two components, namely species richness and evenness (Magurran, 1988). Most common in literature are indices either describing the richness or species number and the evenness or partitioning of individuals over species, or a combination of both (Heip *et al.*, 1998). Diversity indices which are sensitive to sample size cannot be used for comparison of the different microhabitats, because their respective sample sizes differ distinctly. Furthermore, Soetaert & Heip (1990) argued that this dependence is more pronounced in high diversity (e.g.

deep sea) than in low diversity assemblages. Rarefaction curves (Sanders, 1968), calculated using the methods of Hurlbert (1971), were used to compare species richness. This method reduces samples of different sizes to a standard size, in order to make them comparable in terms of the number of species (Heip *et al.*, 1998). Lambshead *et al.* (1983) however pointed out that when there are large differences in sample size, comparison of the corresponding rarefaction curves is limited or even impossible. Furthermore, rarefaction assumes that the spatial distribution of every species is homogeneous (Tipper, 1979). If the distribution of some species is heterogeneous, this method will overestimate the diversity (Thistle, 1998). The slope of the curves is indicative of the evenness of the respective relative abundance distribution (Gotelli & Graves, 1996).

Evenness expresses how evenly the individuals in the community are distributed over the different species. The equitability index J' (Pielou, 1975) however is highly dependent on sample size (Heip *et al.*, 1998) and cannot be used in the present dataset. Therefore, the equitability of the copepod fauna was studied based on the species' abundance distributions as k-dominance curves (Lambshead *et al.*, 1983).

The total species diversity (γ, as measured by species richness or a diversity index) found in a collection of samples can be additively partitioned into the average diversity within samples (α) and among samples (β) (Crist *et al.*, 2003). In the present study, β-diversity is subdivided into β1-diversity which is due to the differences in microhabitat and β2-diversity which is due to the differences in localities. The additive partitioning of species diversity was conducted with PARTITION software (Veech *et al.*, 2002; Crist *et al.*, 2003), taking into account the sediment and coral samples of the coral degradation zone.

A ternary plot was constructed to measure and compare species turnover between microhabitats (restricted to sediment and coral) within boxcores and between boxcores for each microhabitat, as recommended by Koleff *et al.* (2003). The values of a', b' and c' (i.e. the percentage of shared species a, of species exclusively present in the neighbouring sample b and of species exclusively present in the focal sample c) are plotted against a background of β_{sim}-values (Lennon *et al.*, 2001).

Parametric (ANOVA) and non-parametric (Kruskal-Wallis ANOVA and Mann Whitney U test) analysis of variance was performed using the STATISTICA6 software. Bartlett's and Cochran's test were used to verify the homogeneity of variances prior to the analysis.

3.4. RESULTS

In total, the samples from the coral degradation zone and the two coral-free locations yielded 1717 copepods (Table 2). Representatives of six of the ten known copepod orders were found. Harpacticoida made up the bulk of the specimens (>90%) and never occurred with less than 85% of relative abundance in any sample. The other copepod orders were found only sporadically: Calanoida, Misophrioida, Poecilostomatoida and Siphonostomatoida each constituted of less than 1% of the specimens (with 1, 4, 1 and 12 individuals, respectively), Cyclopoida made up 7% (with 125 individuals). The present study focuses on the order of Harpacticoida and, therefore, all other orders are left out of the analyses. Of the 1574 harpacticoid copepods, 913 (or 58%) were adults and 661 (or 42%) were in the copepodite stage. Altogether, 64% of the adult harpacticoids were females and 36% were males.

Sample	Total Copepoda	Total Harpacticoida	Number of harpacticoid adults	Number of species	Average number of adults per species
sed1	62	56	30	21	1,4
sed2	13	13	7	7	1,0
sed3	85	79	34	24	1,4
sed4	29	26	18	15	1,2
sed5	13	13	7	6	1,2
sed6	84	80	37	24	1,5
cor1	200	185	97	47	2,1
cor2	200	181	125	51	2,3
cor3	136	122	78	37	2,1
cor4	200	185	102	44	2,3
cor5	103	93	68	35	1,9
cor6	200	170	102	49	2,1
spo1	123	114	67	34	2,0
spo3	200	189	88	37	2,4
sed7a	20	19	12	10	1,2
sed7b	9	9	6	6	1,0
sed8a	5	5	3	3	1,0
sed8b	35	35	20	16	1,3
Total dataset	1717	1574	901	182	4,95

Table 2. Total number of Copepoda, Harpacticoida, harpacticoid adults, number of species and average number of adults per species within each sample. Samples from the coral degradation zone are ordered according to microhabitat (sed, cor, spo), from the coral-free sediments according to location.

There were no significant differences between harpacticoid densities in the sediment of the coral degradation zone (box 1 and 2) and the sediment of each of the two coral-free locations (Kruskal-Wallis ANOVA, $p = 0.42$). Copepod densities, however, varied strongly within and between both boxcores of the coral degradation zone (mean ± SD: 19 ± 7 and 4 ± 3 per 10 cm^2) and between boxcores 8a and 8b with coral-free sediments (mean ± SD: 2 ± 0.5 and 12 ± 2 per 10 cm^2). In the coral-free sediments, 76.5 % (or 52 individuals) of the harpacticoids were present in the upper first centimeter. The second and third centimeter layer contained 19% (13

individuals) and 3% (3 individuals) of the harpacticoids, respectively. Further analyses are based on adult harpacticoids, due to the impossibility of identifying most of the copepodites. Also, 12 damaged adults were left out because of identification problems.

In the coral degradation zone, the underlying sediment showed a large variation in sediment texture (Table 3). It consisted mainly of fine to medium sand and a more or less pronounced silt fraction, with the median grain size of the sand fraction ranging between 8.3 μm and 194.9 μm. At both coral-free locations, the upper sediment layer consisted of fine to medium sand with a small silt fraction (median grain size ranging between 153.6 and 189.3 μm). With increasing depth, the sediment changed into silt with a limited fine sand fraction (median grain size ranging between 5.1 and 93.6 μm at the third centimeter layer).

	clay (%)	silt (%)	sand (%)	median of sand fraction (μm)
Box3	8,5	19,5	72,0	194,9
Box4	32,7	47,3	20,0	8,3
Box5	15,0	31,9	53,1	75,4
Box6	19,7	34,2	46,1	46,0
Box7a (0-1)	3,8	9,3	86,9	189,3
Box7a (1-2)	4,0	10,6	85,4	168,4
Box7a (2-3)	30,6	49,6	19,8	9,4
Box7b (0-1)	9,2	19,7	71,1	153,6
Box7b (1-2)	23,3	34,9	41,8	29,3
Box7b (2-3)	28,7	43,4	27,9	12,8
Box8a (0-1)	8,4	15,2	76,4	176,0
Box8a (1-2)	47,0	49,8	3,2	4,4
Box8a (2-3)	42,4	48,0	9,6	5,1
Box8b (0-1)	5,1	15,8	79,1	167,2
Box8b (1-2)	7,6	18,8	73,6	160,2
Box8b (2-3)	17,8	26,9	55,3	93,6

Table 3. Granulometric characteristics of the underlying sediment at the coral degradation zone (data for box 1 and 2 are not available), and of the sediment at both coral-free locations.

3.4.1. Harpacticoid copepod composition of the Porcupine Seabight

In total, 901 adult harpacticoids were determined to species level. A list of identified families, genera and species is provided in Appendix. The material examined yielded 182 species, two of which could not be assigned to any family and are treated as Harpacticoida incertae sedis. The remaining 180 species were spread over 20 families. At present, 24 species cannot be assigned unequivocally to a known genus and are assigned to their respective suprageneric taxon (e.g. subfamily Ameirinae). This was inevitable because certain of these species were represented by one sex only, required a profound change in the genus diagnosis or even represented a new genus. The other 156 species were spread over 64 genera, with one genus being new in the

Tetragonicipitidae. All species are taxonomically sound and present no problems in assigning them to their respective higher taxon as defined by the current state of taxonomy.

Because of time limitations and the complexity or extent of certain genera, 84 species were determined to morphospecies-level, i.e. it could not be verified if they were described in literature yet. 98 species were carefully checked against original species descriptions. Of these, 79 species (or 80.6%) are new to science. The identification of certain species (5 of the 19 identified) has to be considered with some reserves (specific names indicated with aff., affinity). In these cases, certain slight morphometric differences (e.g. in length/width ratio of the caudal rami or the exact insertion place of a seta on the first endopodal segment of P1), the presence of one sex only or the paucity of the original descriptions prevented a firm identification.

There is a large variation in the number of species belonging to the different harpacticoid families. Ectinosomatidae, Ameiridae and Argestidae are the most species-rich families (containing 44, 31 and 18 species, respectively). Canthocamptidae, Pseudotachidiidae, Paramesochridae and Idyanthidae are represented by 14, 13, 12 and 10 species, respectively. The following families are represented by seven to two species each (in order of decreasing number of species): Miraciidae, Laophontidae, Cletodidae, Neobradyidae, Zosimidae, Ancorabolidae, Huntemanniidae and Novocriniidae. The remaining five families (Harpacticidae, Normanellidae, Rhynchothalestridae, Tegastidae and Tetragonicipitidae) are monospecific. The most species-rich genera belong to the Ectinosomatidae, Ameiridae and Pseudotachidiidae (i.e. *Pseudobradya* and *Sigmatidium* (each 8 sp.), *Ameira* and *Ameiropsis* (each 6 sp.), *Pseudomesochra* (7 sp.)). Sixteen genera are represented by 3 to 5 species, while most genera contain two species or are monospecific (16 and 27 genera, respectively).

3.4.1.1. Family composition

Five families (Ectinosomatidae, Ameiridae, Pseudotachidiidae, Argestidae and Miraciidae) can be considered as dominating in each of the microhabitats of the coral degradation zone (Figure 3). Each of these families occurred in over 85% of the samples. Together, they represent 75.2% of relative abundance in the sediment and coral samples and 83.9% in the sponge samples. Each of these families does not differ significantly in relative abundance among the microhabitats, except for the family Pseudotachidiidae which occurs with a significantly higher relative abundance on the sponge skeletons (ANOVA, $p = 0.03$). Ectinosomatidae is the most dominant family in sediment and coral samples (24.8% and 29.6%, respectively), while this is the Pseudotachidiidae in the sponge samples (31.0%). The three microhabitats share another five families (Canthocamptidae, Paramesochridae, Laophontidae, Harpacticidae and Neobradyidae), each representing between 0.7% and 5.6% in any of the different microhabitats. These families do not differ significantly in relative abundance among the three microhabitats (ANOVA, $p > 0.05$). Nine families (Idyanthidae, Ancorabolidae, Rhynchothalestridae, Tetragonicipitidae, Zosimidae, Novocriniidae, Cletodidae, Huntemanniidae and Tegastidae) were restricted to one or

two of the microhabitats. However, each of these families was found only sporadically (between 0.2% and 3.9%) in any of the microhabitats.

Altogether, ten families were found in the coral-free sediments, of which Normanellidae had not been found yet in the coral degradation zone. Six of the ten families occur at both locations, being Miraciidae, Ectinosomatidae, Ameiridae, Paramesochridae, Canthocamptidae and Zosimidae. At both locations, Miraciidae and Ectinosomatidae are dominant families, as is the case in the coral degradation zone. However, Paramesochridae and Huntemannidae at coral-free location 7 and Cletodidae at coral-free location 8 appear to be more important families than in the coral degradation zone.

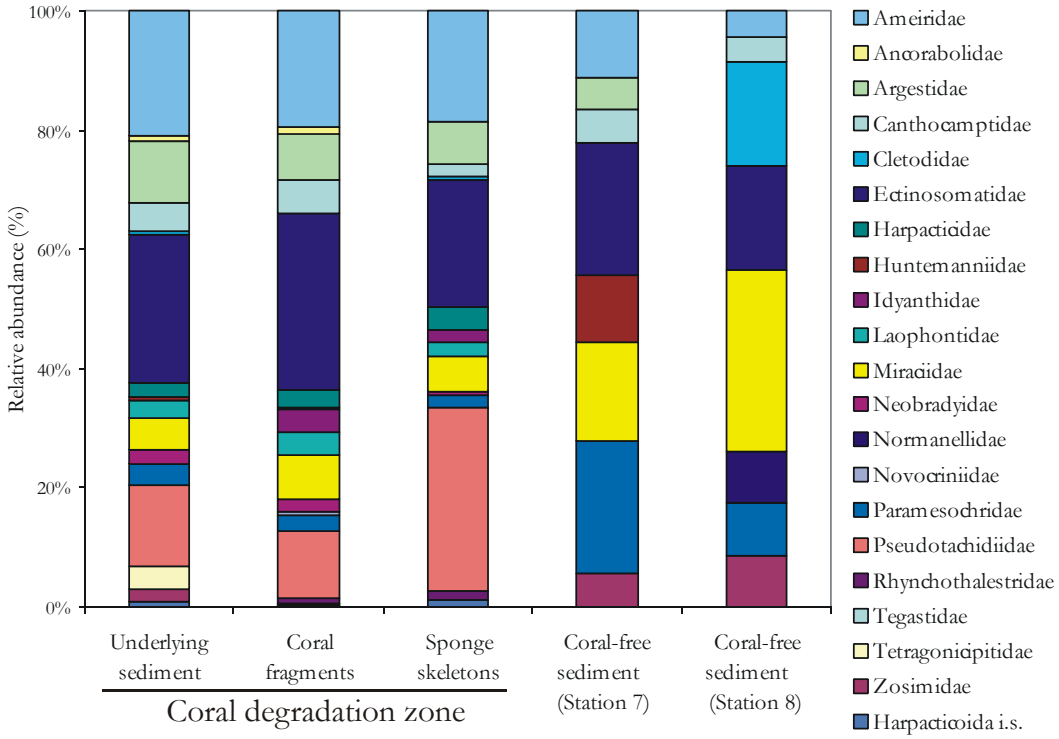


Figure 3. Harpacticoid family composition per microhabitat in the coral degradation zone and both coral-free locations, based on pooled samples per microhabitat.

3.4.1.2. Genus composition

In total, 64 genera were identified. As explained above, 24 species could not be assigned unequivocally to any genus and are treated here as belonging to separate genera. Together with the two species, provisionally placed in Harpacticoida i.s., the maximum number of genera is 90. The sediment, coral and sponge samples of the coral degradation zone contained 47, 67 and 36 genera, respectively. The coral-free sediments of location 7 and 8 yielded 15 and 14 genera, respectively.

No dominant genera are present in the sediment or coral samples (Table 4). *Pseudomesochra*, *Halophytophilus* and *Sigmatidium* (and also *Ameira* and *Pseudobradya* in the coral samples) show a relative abundance between 5% and 10% (and belong to the dominant families

Pseudotachidiidae, Ectinosomatidae and Ameiridae). All other genera never exceed 5% of relative abundance. However, on the sponge skeletons *Pseudomesochra* and *Ameira* (with 31% and 12%, respectively) are found to be dominant genera. Apart from *Microsetella* and *Sigmatidium*, all other genera have a relative abundance of less than 5%. In the coral degradation zone, 21 genera (most of them belonging to Ectinosomatidae, Argestidae, Ameiridae and Miraciidae) were present in each of the three microhabitats. The genera restricted to one of the microhabitats (9, 22 and 6 genera in sediment, coral and sponge samples, respectively) were found only sporadically and never exceeded 2.5% of relative abundance in their respective microhabitat. Also, any of the genera shared between sediment-coral (16), coral-sponge (8) and sediment-sponge (1) never exceeded 4% of relative abundance in any of the microhabitats.

In the coral-free sediments, 25 genera were identified. The genera *Kliopsyllus*, *Talpina*, *Robertgurneya*, *Sagamiella* (and also Canthocamptidae sp. 9, Canthocamptidae sp. 10 and Paramesochridae sp. 1) had not been found yet in the coral degradation zone.

Genus	Underlying sediment (%)	Coral fragments (%)	Sponge skeletons (%)
Ameira	3,01	8,22	11,61
Amphiascus	3,76	3,67	4,52
Bradya	2,26	0,70	1,29
Dizahavia	2,26	0,52	1,94
Ectinosoma	1,50	2,10	0,65
Eurycletodes	0,75	0,52	2,58
Filexilia	2,26		
Fultonia	0,75	3,85	
Halophytophilus	7,52	5,24	2,58
Idyanthe		2,62	1,94
Klieosoma	1,50	1,57	3,23
Laophonte	2,26	3,67	2,58
Leptomesochra	4,51	1,40	2,58
Leptopsyllus	2,26	0,52	
Mesocletodes	3,76	0,35	
Microsetella	0,75	0,87	6,45
Neobradyidae gen. 1	2,26	0,52	
Perissocope	2,26	3,15	3,87
Pseudameira	3,76	0,70	
Pseudobradya	3,76	8,04	0,65
Pseudomesochra	9,02	8,22	30,97
Sarsameira	0,75	3,15	0,65
Sigmatidium	6,02	9,97	5,81
Stenocopia	2,26	1,75	0,65
Tetragonicipitidae gen. 1	3,76	0,17	
Xylora	3,01	1,40	
Zosime	2,26	0,35	
Total number of genera	47	67	36

Table 4. Harpacticoid genera (with a relative abundance of minimum 2% in at least one microhabitat) from the cold-water coral degradation zone, per microhabitat.

3.4.1.3. Species composition

Only two species, *Sigmatidium* sp. 6 (Ectinosomatidae) and *Pseudomesochra* sp. 4 (Pseudotachidiidae) each accounted for 5% of the complete dataset (Fig. 4). 25 species each had a relative abundance between 1% and 4.2%. The remaining 155 species each occurred with less than 1% of relative abundance. The average number of individuals per species is 5 and 72 species were present as singletons. If one replotted Figure 4 as a cumulative abundance graph, 20 species (11%) would contain 50% of the individuals. The sediment, coral and sponge samples of the coral degradation zone yielded 74, 122 and 54 species, respectively. The coral-free sediments of location 7 and 8 contained 16 and 18 species, respectively.

In the sediment and coral samples of the coral degradation zone, no dominant species are present. There is only one species in the sediment that barely exceeds 5% of relative abundance (*Halophytophilus* sp. 2 at 5.3%), while there are two such species in the coral samples (*Pseudobradya* sp. 3 at 6.1% and *Sigmatidium* sp. 6 at 5.9%). The remaining species (73 in the sediment and 120 on the coral fragments) each occur with a low relative abundance (below 5%). The sponge samples yielded 54 species, of which two species of *Pseudomesochra* are relatively abundant (*Pseudomesochra* sp. 1 with 13.5% and *Pseudomesochra* sp. 4 with 8.4%). *Ameira* sp. 3, *Microsetella* sp. 1 and *Ameira* sp. 1 just exceed 5% of relative abundance. None of the species exclusive to one of the microhabitats (21, 56 and 11 in the sediment, coral and sponge samples, respectively) exceeds 2.5% of relative abundance in its respective habitat. None of the species, shared between sediment-coral (27), coral-sponge (17) and sediment-sponge (4), exceeded 4% of relative abundance in any of the microhabitats.

In total, 34 species were found in the coral-free sediments, ten of which were shared with the coral degradation zone. None of the species was present at both coral-free locations.

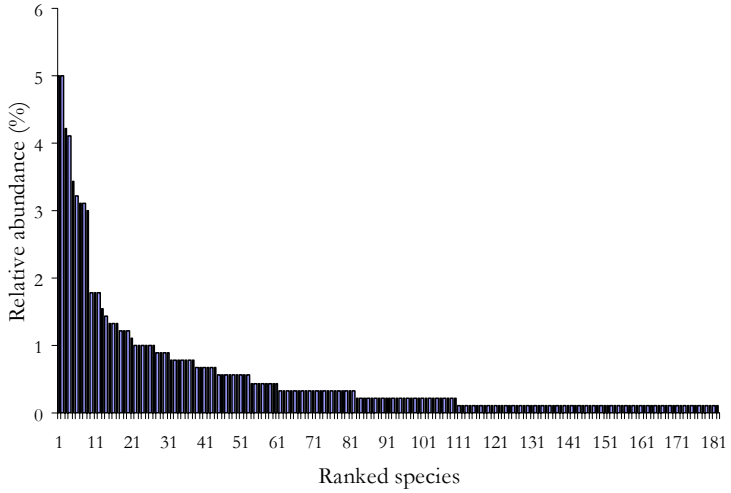


Figure 4. Rank-order of abundance histogram. The height of the bar for each species represents its relative abundance when all samples are pooled.

3.4.2. Similarity analysis

At the family level, the MDS graph of the complete dataset (Fig. 5A) shows a clustering of coral, sponge and half of the sediment samples of the coral degradation zone. Three samples of coral-free sediments are separated from the coral degradation zone clustering and form a group themselves. It is confirmed with ANOSIM that the CDZ samples are separated from the coral-free samples ($R = 0.799$, $p = 0.002$). The average dissimilarity in composition is 61.3% and mainly attributed to a higher abundance of Miraciidae, Ameiridae and Pseudotachidiidae (explaining 14.9%, 14.6% and 10.7% of the dissimilarity, respectively) in the CDZ and to a higher abundance of the families Huntemanniidae, Cletodidae and Zosimidae (explaining 6.9%, 4.2% and 3.7% of the dissimilarity, respectively) in the coral-free sediments (as shown by SIMPER). Indicator family analysis produced significant indicator values for two families: Paramesochridae had a preference for coral-free sediments (IV = 88.5, $p = 0.003$) and Pseudotachidiidae had a preference for the CDZ (IV = 85.7, $p = 0.007$).

A second MDS graph, restricted to samples from the CDZ (Fig. 5B), shows all samples plotted at comparable distances from each other with sediment samples placed circumferentially around the coral samples. No separate groups can be discerned.

In a third MDS graph, samples are again plotted in a similar way, with the coral samples clustered and the sediment samples scattered (Fig. 5C). Pairwise comparison of the groups with ANOSIM was only significant for sediment-coral ($p = 0.033$) and showed these microhabitats as not clearly separated ($R = 0.321$). Also, average dissimilarity in composition was rather low (36.3%), and mainly attributed to a higher abundance of Ameiridae, Pseudotachidiidae, Argestidae and Ectinosomatidae (explaining 13.5%, 12.8%, 11.7% and 10.4% of the dissimilarity, respectively) on the coral fragments and the higher abundance of Tetragonicipitidae (explains 5.4% of the dissimilarity) in the underlying sediment (as indicated by SIMPER). Indicator family analysis showed that Idyanthidae has a significant preference for the coral fragments (IV = 100, $p = 0.004$).

At the genus level, pairwise comparison of the groups (ANOSIM) in the CDZ (without sed2 and sed5) was only significant for sediment-coral ($p = 0.005$) and indicated these microhabitats as overlapping and barely separated ($R = 0.532$). The average dissimilarity in composition between underlying sediment and coral is 67.8% and mainly attributed to the higher abundance of *Pseudomesochra*, *Halophytophilus* and *Pseudobradya* (explaining 7.3%, 4.5% and 4.3% of the dissimilarity, respectively) on the coral fragments and the higher abundance of *Mesocletodes*, *Leptomesochra* and Tetragonicipitidae gen. 1 (explaining 4.6%, 3.5% and 3.0% of the dissimilarity, respectively) in the underlying sediment. Indicator genus analysis showed that six genera had a significant preference for the coral fragments (*Ameiropsis* (IV = 83.3), *Fultonia* (IV = 100), *Mesochra* (IV = 83.3), *Idyanthe* (IV = 83.3), *Haloschizopera* (IV = 83.3) and *Marsteinia* (IV = 83.3)). Only one genus, *Xylora* (IV = 74.7), had a significant preference for the sediment.

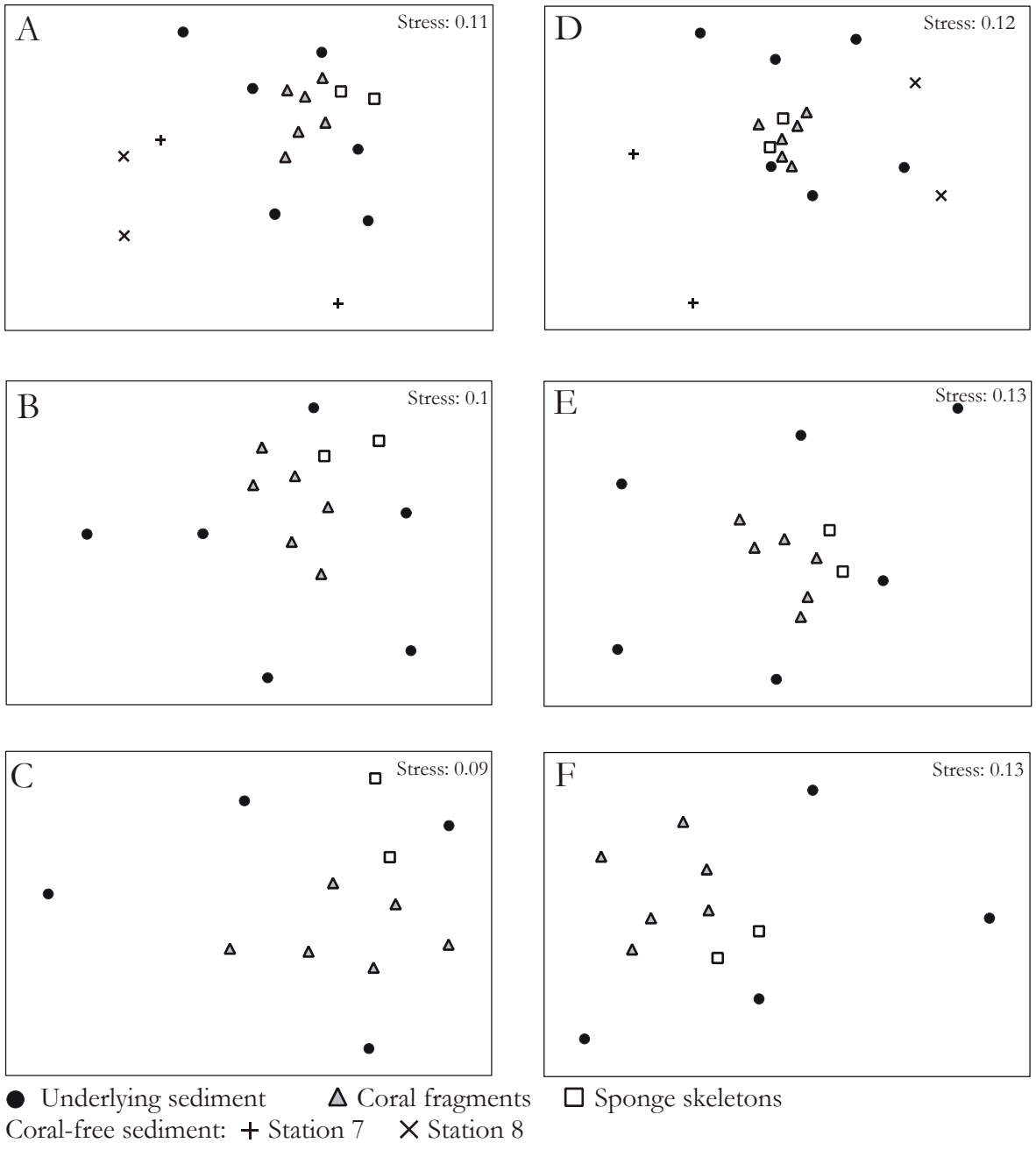


Figure 5. MDS two-dimensional ordination plots. Stress values are indicated. (A-C at the family-level, D-F at the species-level). (A,D) all samples; (B,E) samples from the coral degradation zone; (C,F) samples from the coral degradation zone without sed2 and sed5.

At the species level, the MDS graph of the complete dataset (Fig. 5D) shows the coral, sponge and two of the sediment samples from the coral degradation zone plotted together, with the remaining sediment samples and samples from both coral-free locations widely scattered around. No groups can be discerned except for the central clustering of all coral and sponge samples and two sediment samples.

The MDS graph of all samples from the CDZ (Fig. 5E) produces a similar pattern with coral and sponge samples closely plotted together and sediment samples scattered circumferentially at

varying distances from the central cluster. ANOSIM also indicates the absence of significant differences between the microhabitats.

In a third MDS graph (without sed2 and sed5) a similar pattern is produced with coral and sponge samples near to each other and sediment samples at somewhat larger distance plotted (Fig. 5F). Pairwise comparison of the groups with one-way ANOSIM was only significant for sediment-coral ($p = 0.005$) and showed these microhabitats as overlapping and barely separable at all ($R = 0.48$). The average dissimilarity in composition between underlying sediment and the coral fragments is high (80.2%) and mainly attributable to the higher abundance of *Pseudobradya* sp. 3, *Ameira* sp. 1, *Halophytophilus* sp. 2 and *Pseudomesochra* sp. 4 (explaining 4.2%, 3.8%, 3.7% and 2.7% of the dissimilarity, respectively) on the coral fragments and the higher abundance of *Pseudomesochra* sp. 1 and Tetragonicipitidae gen. 1 sp. 1 (explaining 2.7% of the dissimilarity each) in the underlying sediment, as indicated by SIMPER. However, similarity between sediment samples (14.6%) and between coral samples (35.5%) is rather low.

Corresponding analyses with presence/absence data produced similar patterns. This illustrates that the low values of the species' relative abundances only add little information. Two-way crossed ANOSIM (including all sediment and coral samples of the CDZ) showed no significant effect of the locations of the boxcores (on the mound flank or in the channel between the mounds).

3.4.3. Diversity analysis

The rarefaction curves of the separate samples from the coral degradation zone indicate that the differences in species richness are relatively small (Fig. 6A). The sponge samples appear to have a slightly lower diversity. The mean value (± SD) of the expected number of species for 50 individuals [ES(50)], based on rarefaction curves of every coral and sponge sample, was 30.1 ± 1.0 for coral and 27.1 ± 1.0 for sponge. Because none of the sediment samples contained more than 50 adults, the mean of ES(50) for the sediment could not be calculated. The sediment curves coincide with the coral curves and are characterised by a similar slope. To test for a difference between microhabitats, a Mann-Whitney U test was performed at each knot common to all samples in the comparison. If all tests were significant, then the diversity at the different habitats was considered to differ significantly (Thistle, 1998). This proved the absence of a significant difference in species-diversity (ES) between sediment and coral samples. This method could not be applied with incorporation of the sponge substrate, because there are only two sponge samples. The curves of the sediment samples are short and end in a range where distinction between the curves is difficult. Although they might indicate a species richness which is as high as in the coral samples, larger samples are needed to firmly decide on the similarities or differences of their respective diversity. Because all rarefaction curves tend to converge at low abundances, no distinction between different richness patterns can be drawn if sample sizes are not sufficient (Tipper, 1979) and this is likely to be the case with the sediment samples. The rarefaction curves

of the coral-free sediments are not plotted on Figure 6A because they are too short and completely coincide with the sediment and coral curves of the coral degradation zone.

Rarefaction curves of the pooled data per substrate (Fig. 6B) show a different pattern in which the sediment has the highest diversity. The sponge substrate is characterised by a lower diversity, which agrees with the findings of the separate rarefaction curves. Although the samples of both coral-free locations both lack the presence of coral fragments, the data of both locations are not pooled because the effect of water depth cannot be ignored.

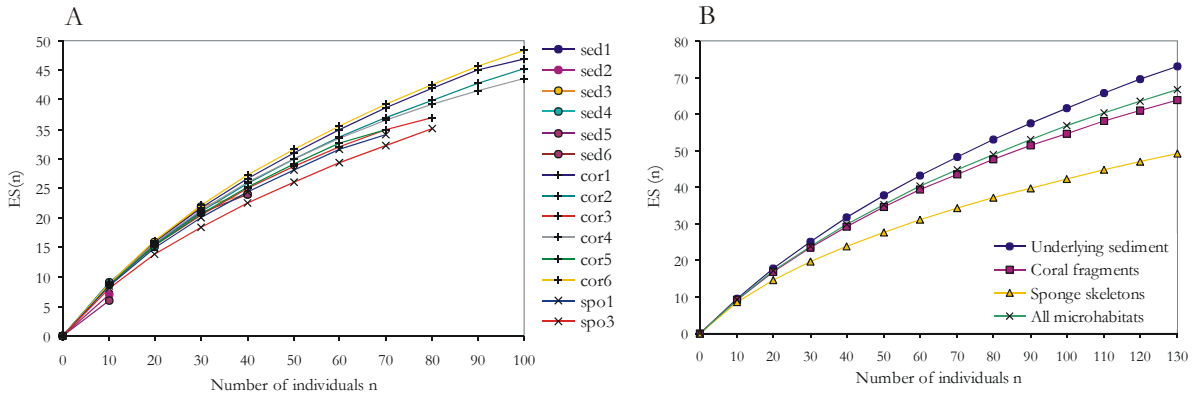


Figure 6. Rarefaction curves of (A) all separate samples from the coral degradation zone and (B) for the pooled data per microhabitat.

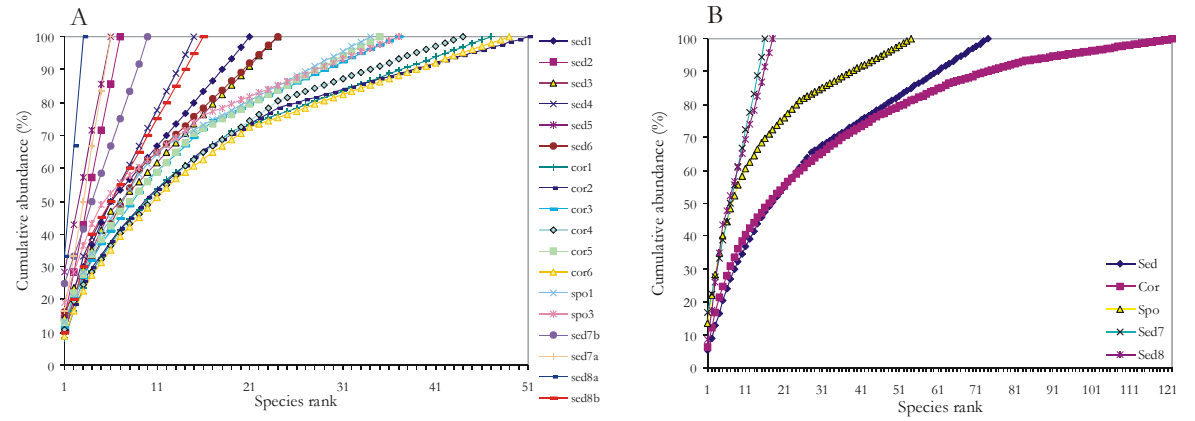


Figure 7. K-dominance curves of (A) all separate samples from the coral degradation zone and both coral-free locations and (B) of the pooled samples per microhabitat.

Distinction between the different k-dominance curves of the separate samples (Fig. 7A) is difficult because most curves are crossing. The upper curves are bent upwardly due to their small sample size. The crossing of each of the curves with the Y-axis equals the relative abundance of the most dominant species. For certain sediment samples (e.g. sed2 and sed5), these values are rather high because of the small sample size. The relative abundance of the most dominant species in one of the sponge samples reaches 19.3%, while for the other sponge sample and the different coral and sediment samples (except sed2 and sed5) of the coral degradation zone this ranges between 8.2% and 16.2%. Caution is appropriate when interpreting the final number of

species identified for each of the k-dominance curves. This final species rank will increase with increasing number of specimens identified. The diversity between the separate samples of the different microhabitats cannot be compared in strict terms due to the intersections (Lambshead et al., 1983). The curves however are so close that a realistic interpretation would be that there is little difference and that all curves represent a high equitability.

K-dominance curves of the pooled data (Fig. 7B) show the dominance in the sponge samples to be slightly higher than in the coral and sediment samples. Coral and sediment samples intersect because of the lower sampled number of individuals from the sediment. This effect straightens the upper part of the sediment curve. Intersecting curves are strictly speaking incomparable (Lambshead *et al.*, 1983), but their similar slope and shape indicate a high equitability in both sediment and coral. The curves of the coral-free sediments are highly influenced by the small sample size, but their shape also suggests a high evenness.

Total species richness (γ) of the coral degradation zone is mainly determined by β-diversity due to locations (Fig. 8). In contrast, 75% of the Shannon index is explained by α diversity within samples, while locations contribute only 17%. By adding locations species richness is greatly enhanced. The Shannon index however shows these species to be rare, as most of the diversity is explained by α, which means that the same 'common' species occur across the different locations. β diversity which is due to the differences in microhabitat is small as expressed by both measures.

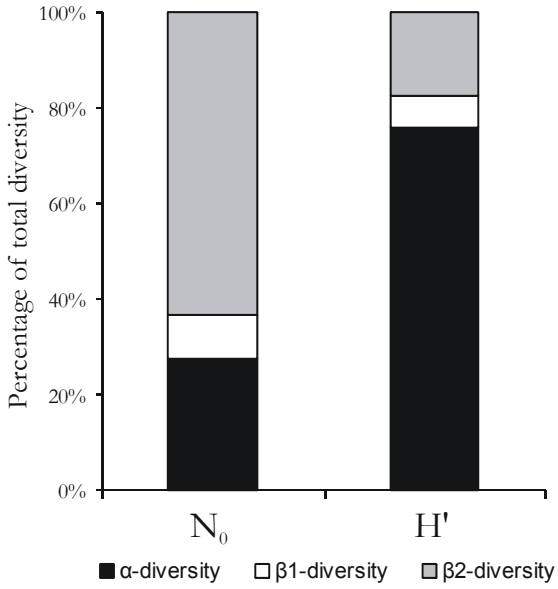


Figure 8. Additive partitioning of total diversity for species richness N_0 and Shannon-Wiener diversity H'. β1-diversity is the fraction of β-diversity due to the differences in microhabitat. β2-diversity is the fraction of β-diversity due to the differences in localities.

In the ternary graph (Fig. 9), the plots showing turnover between both microhabitats are accumulated in the lower right corner of the graph, which illustrates that within each boxcore a high percentage of the species is exclusively present in the coral sample and only a low percentage is restricted to the sediment sample. Species turnover between locations is significantly higher for sediment samples than it is for coral samples (ANOVA, $p = 0.000$). Species turnover between both microhabitats at each of the locations is significantly lower than species turnover between locations for the sediment samples (ANOVA, $p = 0.001$). The third microhabitat (sponge skeletons) was sampled only in two boxcores. Species turnover between sponge and each of the two other microhabitats was also high, with β_{sim} ranging between 0.69 and 0.73 (not plotted). Within the coral degradation zone, a pattern in which an increased distance between two boxcores is reflected in a higher species turnover does not seem to exist. No species were shared between both locations of coral-free sediments, nor between these two locations and any of the sediment samples of the coral degradation zone.

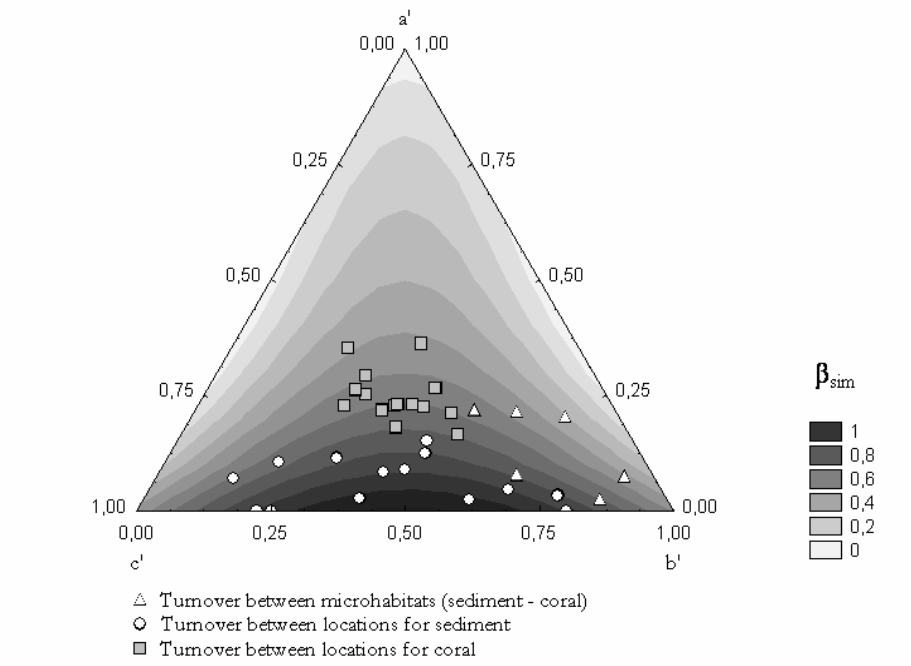


Figure 9. Ternary graph representing species turnover between coral and sediment within the same location and between locations for both sediment and coral samples. Shading visualises the values of β_{sim}.

3.4.4. Distribution of the known copepod species of the Porcupine Seabight

As already mentioned above, 19 of the 98 species (or 19.4%), that were carefully checked against original species descriptions, could be identified and are listed hereafter, with the number of specimens found between parentheses:

Ancorabolidae	*Laophontodes mourois* Arroyo, George, Benito & Maldonado, 2003 (5)
	Lobopleura expansa (Sars, 1908) (3)
Argestidae	*Eurycletodes* aff. *similis* (T. Scott, 1895) (7)
	Fultonia aff. *bougisi* Soyer, 1964 (12)
	Mesocletodes guillei Soyer, 1964 (1)
	Mesocletodes irrasus (T. & A. Scott, 1894) (1)
Canthocamptidae	*Mesochra pygmaea* (Claus, 1863) (9)
Ectinosomatidae	*Klieosoma triarticulatum* (Klie, 1949) (8)
	Microsetella norvegica (Boeck, 1865) (16)
Idyanthidae	*Idyanthe dilatata* (Sars, 1905) (5)
	Idyella major Sars, 1920 (1)
	Nematovorax gebkelinae Bröhldick, 2005 (2)
Laophontidae	*Laophonte elongata* Boeck, 1872 (5)
Novocriniidae	*Atergopedia vetusta* Martínez Arbizu & Moura, 1998 (3)
Paramesochridae	*Diarthrodella* aff. *orbiculata* Klie, 1949 (1)
	Scottopsyllus aff. *robertsoni* (T. & A. Scott, 1895) (1)
Zosimidae	*Zosime bergensis* Drzycimski, 1968 (5)
	Zosime paramajor Bodin, 1968 (1)
	Zosime aff. *pacifica* Fiers, 1991 (1)

3.4.4.1. Distribution of known species of Ancorabolidae

The present report of the dorsoventrally flattened *Lobopleura expansa* is the rediscovery of the species since its description by Sars (1908) from the Saltenfjord (Norway). Recently, Conroy-Dalton (2004) proved that other records from Lang (1948) (Gulmarfjord, Sweden) and Roe (1958) (Ireland, on *Laminaria digitata* holdfasts) in fact were of the closely related *L. ambiducti* Conroy-Dalton, 2004. This species was collected and described from interstitial water of a sandy beach on Isle of Iona (Scotland) (Conroy-Dalton, 2004). The same author also recorded *L. ambiducti* from Ireland. The second known ancorabolid species, *Laophontodes mourois*, was described from the northern coast of Spain at a depth of 12 m and collected from the holdfasts of the macroalga *Laminaria ochroleuca* (Arroyo *et al.*, 2003). In this fraction of the macrophytes, several habitats however appear combined (phytal, epiphytes, considerable amounts of sediment), and it was unclear whether this species belonged to the psammal or was detached from some other substrate, such as sponges and other sessile macrofauna on the algae (Arroyo *et al.*, 2003).

3.4.4.2. Distribution of known species of Argestidae

Recently, George (2004) presented a list of all known argestid species, including data on their geographic and bathymetric distribution. Although species of this family occur from the sublittoral down to abyssal depths, the Argestidae have a preference for deep-sea habitats and generally prefer soft instead of sandy substrata (George, 2004). Based on distribution records, Argestidae are considered to have a worldwide distribution (George, 2004). With 18 species, the Argestidae form a species-rich family in the Porcupine Seabight. *Fultonia bougisi* and *Mesocletodes guillei* both are described from the Mediterranean (Soyer, 1964), with the former species reported down to 610 m water depth. George (1999) also reported *F. bougisi* from the Magellan Region. *Mesocletodes irrasus* and *Eurycletodes similis* have a distribution covering the Atlantic Ocean and Northern Subpolar Seas from various depths (Lang, 1948; George, 2004), with *M. irrasus* extending its distribution into the Mediterranean (Soyer, 1964).

3.4.4.3. Distribution of known species of Canthocamptidae

Mesochra pygmaea has been reported from numerous localities in the NE Atlantic and the Mediterranean (including the Black Sea) and also occurs along the western side of the North Atlantic (Bermuda Isles) (Lang, 1948; Pesta, 1959). It has been reported from between algae, in sandy and muddy bottoms, and knows a large vertical distribution (to 286 m depth) (Lang, 1948). Furthermore, Hamond (1971) examined specimens from all over the world (Arctic waters, eastern coast of U.S., Mozambique, southern Australia) and found hardly any differences except in secondary ornamentation.

3.4.4.4. Distribution of known species of Ectinosomatidae

In the Porcupine Seabight, 12 ectinosomatid genera were identified, four of which are characterised by a pair of prehensile first legs (i.e. *Bradyellopsis*, *Halophytophilus*, *Klieosoma* and *Peltobradya*). Known species of *Bradyellopsis*, *Halophytophilus* and *Klieosoma* are mostly reported from the washings of littoral algae, suggesting a shift to hyperbenthic algal biotopes from the sedimentary benthic substrates more typical of the Ectinosomatidae (Noodt, 1971; Hicks & Coull, 1983; Watkins, 1987). The single described species of *Peltobradya* is an associate of a bryozoan host in the Mediterranean Sea (Medioni & Soyer, 1967). *Klieosoma triarticulatum* occurs on *Laminaria* in Helgoland (Klie, 1949; Hicks & Schriever, 1985). *Microsetella norvegica* has colonised the marine plankton and is widely distributed across the globe, especially in shallow coastal waters (Lang, 1948; Boxshall, 1979).

3.4.4.5. Distribution of known species of Idyanthidae

Species of Idyanthidae are regularly found in the deep sea (Seifried, 2004). *Idyanthe dilatata* has been described from the west coast off Norway in depths ranging from 18 to 54 metres (10 to 30 fathoms) (Sars, 1905). Furthermore, it has been reported at higher latitudes, in the White Sea (Chislenko, 1967) and Spitzbergen (Mielke, 1974). *Idyella major* has been reported from south

Norway (Kristiansand) and Gulmarfjord (Sweden) (Lang, 1948). *Nematovorax gebkelinae* has recently been described from the soft-bottom deep sea of the Angola Basin in the South Atlantic (at depths of around 5400 m) and is the single described species in its genus (Bröhldick, 2005). The present report extends its distribution area to the North-East Atlantic and up to a depth of 880 m (Box 6).

3.4.4.6. Distribution of known species of Laophontidae

Lee & Huys (1999) recently reviewed all bathyal records of the family Laophontidae. In general, Laophontidae have rarely been reported from bathyal habitats. The majority of laophontid genera inhabit the intertidal zone or shallow subtidal localities. Recently however, several genera were described from Antarctic deep waters (*Archilaophonte* Willen, 1995, *Cornylaophonte* Willen, 1996 and *Weddellaophonte* Willen, 1996) and deep-sea hydrothermal vents near the Azores in the Atlantic Ocean and north of Easter Island in the Pacific Ocean (*Bathylaophonte* Lee and Huys, 1999), with *B. pacifica* Lee & Huys, 1999 representing the deepest record of Laophontidae at 2572 m water depth. The association of *Bathylaophonte* with hydrothermal vent fields is likely to be coincidental (Lee & Huys, 1999). Other records of Laophontidae from the bathyal zone, i.e. between 200 and 4000 m water depth, are from 5 different species of the genus *Laophonte*, and all refer to high latitude localities, both in the Northern (Norway (Drzycimski, 1969) and Sweden (Por, 1964)) and Southern (Antarctic (Brady, 1910)) hemispheres. Apart from a record from Bergen (Norway) at 512 m water depth (Drzycimski, 1969), *Laophonte elongata* also has been reported from various localities in the NE Atlantic and the Mediterranean Sea and occurs between algae and on muddy bottoms (Lang, 1948; Noodt, 1958).

3.4.4.7. Distribution of known species of Novocriniidae

At present, the family Novocriniidae only consists of two species with one of which, *Atergopedia vetusta*, described from the Arctic Ocean at a depth of 534 m (to the north-west of Franz-Josef Land). It was collected from muddy sediments covered by a mat of sponge spicules (Martínez Arbizu & Moura, 1998a). The present report extends its distribution area down south in the Atlantic Ocean.

3.4.4.8. Distribution of known species of Paramesochridae

Although Paramesochridae traditionally were thought to be typically interstitial shallow-water, several studies now have reported the family from the deep sea (Becker, Noodt & Schriever 1979; Ahnert & Schriever 2001; Veit-Köhler, 2005). *Diarthrodella orbiculata* Klie, 1949 has been described from Helgoland (Klie, 1949). Bocquet & Bozic (1955) described *Idyanthopsis psammophila* from Roscoff, which was considered a synonym of *D. orbiculata* by Kunz (1962) (but not by Bodin (1997)). *Scottopsyllus robertsoni* is described from Firth of Forth (Scotland) (T. Scott, 1895) and has also been reported from the Black Sea (Bulgaria) (Apostolov, 1972).

3.4.4.9. Distribution of known species of Zosimidae

Only 17 species of Zosimidae are described to date, of which 13 were found in the deep sea (Seifried, 2004). Hundreds of undescribed species, mainly from the deep sea and the continental slope, are awaiting description (Seifried, 2003). In this study, one of the four species of *Zosime* is new to science. *Zosime pacifica* is described from the Pacific Ocean off the Californian coast occurring at depths ranging from 50 to 565 m (Fiers, 1991c). However, as only one female individual was found, this identification has to be considered with some reserves. *Zosime bergensis* has been recorded from various localities in the fjords and coastal waters of western Norway, from sand and mud at water depths between 105 and 680 m (Drzycimski, 1968). Female and male of *Zosime paramajor* were described from the Bay of Biscay at 900 m water depth (Bodin, 1968) and the deep sea off North Carolina (Coull, 1973), respectively.

In summary, most of the species have been reported from various localities along the NE Atlantic shores and from higher latitudes in the Northern Subpolar and Polar Seas. Only two species can be considered cosmopolitan (*Mesochra pygmaea* and *Microsetella norvegica*). Up to now, seven species were known from their type-locality only, with *Nematovorax gebkelinae* (from Angola Basin) and *Zosime pacifica* (from California, Pacific Ocean) the most remarkable in view of their remote finding place. Also, five species were previously reported from the Mediterranean Sea, one from the Black Sea, one from the Magellan region and one from the deep NW Atlantic. Five species (*Nematovorax gebkelinae*, *Atergopedia vetusta*, *Zosime bergensis*, *Z. paramajor*, *Z. pacifica*) are deep-sea species, although other species (such as *Fultonia bougisi*, *Eurycletodes similis*, *Mesochra pygmaea* and *Laophonte elongata*) are also capable of penetration into deeper waters. It is interesting to note that Lang (1948) reported *Eurycletodes similis* from the '*Lophahelia*-Riff' (obviously *Lophelia*) near Bohuslän (west coast of Sweden). Furthermore, two species (*Laophontodes mourois* and *Klieosoma triarticulatum*) have been described from *Laminaria* algae suggesting a phytal affinity.

3.5. DISCUSSION

The present study is the first characterisation of the harpacticoid copepod fauna associated with cold-water coral substrates in the deep sea. Previous studies have focused on the associated metazoan meiofauna (Raes & Vanreusel, 2005) and nematofauna (Raes & Vanreusel, 2006) of *Lophelia pertusa* reef degradation zones in the Belgica Mound province (Porcupine Seabight, North-East Atlantic). Raes & Vanreusel (2005) concluded that the presence of large biogenic structures on the seafloor enables more taxa to be present and particularly favours harpacticoid copepods, naupliar larvae and polychaetes, as in the meio-epifaunal community these taxa have a higher relative abundance than in the underlying sediment. This is a pattern similar found in epiphytic communities where a shift to a predominance of harpacticoids and naupliar larvae has been reported, especially on seagrass leaves and macro-algae (Coull *et al.*, 1983; Bell *et al.*, 1984; Hall & Bell, 1993; De Troch *et al.*, 2001a). The main aim of the present study is to investigate whether distinct copepod assemblages are associated with the different microhabitats (i.e. dead coral fragments, glass sponge skeletons and underlying sediment) present in the coral degradation zone.

Bett *et al.* (1994) and Shirayama & Fukushima (1995) tested the sampler bias caused by sampling with boxcorer (Hessler & Jumars, 1974). They confirmed that the multiple corer (Barnett *et al.*, 1984) is the best device available for sampling of open-sea, soft-bottom sediments (Blomqvist, 1991). The biogenic substrates examined in this study however prevent the use of multiple corer, and one should keep in mind that the used boxcorer could have introduced sampling bias by washing away loose, light material containing associated fauna. Different species might have a different susceptibility to this disturbance. Thistle & Eckman (1990a) even pointed out the possibility that sexes of one species could differ in erodibility to explain the more extreme reports of male rareness in literature. As a consequence of this bias, comparing density measures with literature should be done cautiously.

Pfannkuche (1985) reported harpacticoid densities from a transect (using multiple corer) along the nearby northwestern slope of the Porcupine Seabight. One station was located at a depth of 960 m and yielded 33 ± 15 harpacticoids/10 cm². Although our reports from the underlying sediment in the coral degradation zone show some variation, they do not differ markedly from this. Moreover, in a review of the benthos of the North-East Atlantic, Vincx *et al.* (1994) showed that low copepod abundances are encountered in all zones and at all depths. This might be attributed to the patchy distribution of copepods (Dinet *et al.*, 1985).

Strict comparison with densities on the coral fragments and sponge skeletons is impossible because the exact surface area of these complex substrates could not be defined. Raes & Vanreusel (2005) however inferred the sediment-clogged coral framework to be more densely populated by meiofauna than the underlying sediment because it is able to trap sedimented organic food. Therefore, it could be regarded as a hotspot of abundant food in a generally food-limited environment.

3.5.1. Harpacticoid copepod composition and microhabitat preferences

Our similarity analyses showed that coral fragments and underlying sediment do not harbour distinctly different copepod assemblages. MDS-plots at different taxonomic levels produced a similar pattern of coral samples clustered centrally, with sediment samples scattered circumferentially. Low R-values (ANOSIM, only significant after omitting two small outlying sediment samples) and low dissimilarity values (SIMPER) indicated a considerable degree of overlap and the microhabitats as not clearly separated by their faunal composition. Sediment texture varies strongly between the different sampled boxcores in the coral degradation zone. This might result in a strong variation of the sediment assemblage that would be shown as a wide scattering of the sediment samples in the MDS plots. However, in deep-sea studies it is a common problem that the circumstances of low animal abundance and high diversity make it particularly difficult to detect spatial changes in community structure without taking a large number of samples. The high evenness, typically found in the deep sea (Rose *et al.*, 2005), in combination with the limited sample sizes undoubtedly influences the pattern observed. Due to the species' low relative abundances, the presence of species in small samples may largely be due to chance. Also, rarefaction curves indicate the fauna to be under sampled (see below) and the extent to which the observed pattern reflects sampling error is unclear.

However, sediment samples do not cluster in opposition to the coral samples and appear to be more similar to any of the coral samples (not necessarily from the same boxcore) than to any of the other sediment samples. Species turnover between sediment samples from different boxcores also is higher than between sediment and coral fragment within a boxcore, and between coral fragments from different boxcores. This indicates that most species found in the underlying sediment also occur on the overlying coral fragments and only rarely are encountered in sediment of a nearby location. Furthermore, the diversity due to the differences in microhabitat ($\beta 1$) is small. As the additive partitioning of diversity unifies the disparate approaches of studying diversity and composition (Crist *et al.*, 2003), the low values of $\beta 1$ might suggest that, within the coral degradation zone, copepod diversity and composition are rather similar in sediment and on coral fragments and do not contain distinctly different assemblages. Although the large variation of the sediment fauna may largely be due to the horizontal heterogeneity in the distribution of deep-sea harpacticoids (Thistle 1978, 1980), it is clear that the sediment species composition is strongly influenced or contaminated by the fauna present on the overlying coral fragments. As only two sponge samples were collected, this strongly impedes any conclusions drawn on the assemblage it contains.

Raes & Vanreusel (2006) conversely found that the nematode assemblages associated with these three microhabitats are significantly different from each other. They argued the assemblages were fundamentally structured by the physical disturbance of strong currents. Typical epifaunal taxa, such as the opportunistic Epsilonematidae and Draconematidae, were especially abundant on the dead coral fragments, while most nematodes in the sediment-dwelling community belong to the slender morphotype typical for an interstitial microhabitat (Giere, 1993).

The qualitative comparison, based on pooled data per microhabitat, showed a remarkably similar family composition in all three microhabitats, apart from a higher dominance of Pseudotachidiidae on the sponge skeletons. The families Ectinosomatidae, Ameiridae, Pseudotachidiidae, Argestidae and Miraciidae are considered to be dominant in each of the habitats. Separate sediment samples are quite different in family composition, but again this most likely is the result of the limited sample size. With an increase of taxonomic resolution, comparison becomes more difficult because relative abundances of the taxa decrease. Genus composition of underlying sediment and coral fragments again is highly similar, the sponge skeletons are characterised by the pronounced dominance of *Pseudomesochra*. Most of the genera however occur with low relative abundances of less than 5% each. In deep-sea samples, the overwhelming majority of species (>90%) generally make up less than 2% of the total abundance each (e.g., Hessler & Jumars, 1974; Grassle & Maciolek, 1992). In the Porcupine Seabight, 85% of the harpacticoid species even occurred with less than 1% of relative abundance each. Because of these low relative abundances, inferring habitat preferences at the species level is strongly restricted.

Hicks & Coull (1983) pointed out the remarkable specificity of familial, and in many instances generic and specific associations of harpacticoids with particular habitat types. Especially in the inter- and subtidal, it has been shown that harpacticoids are able to exploit differently the different microhabitats provided by e.g. macroalgae or seagrasses (De Troch *et al.*, 2003; Arroyo *et al.*, 2006). Certain families and genera are known to constitute typical 'phytal' assemblages and these are usually quite distinct from often closely adjacent sedimentary habitats (Hicks, 1985). Furthermore, Hicks (1977b) referred to two general sub-associations of harpacticoids in the phytal, i.e. those characteristic of the sediment trapped by the algae and the true phytal-dwelling forms of which the most specialised families are dorso-ventrally flattened or laterally compressed. In the deep sea, several studies have found that the abundances and spatial distributions of certain harpacticoid species are correlated with biologically produced structures like polychaete mudballs and xenophyophore tests (Thistle, 1982; Levin & Thomas, 1988). Several possible mechanisms underlying these associations have been suggested, such as the potential habitat or refuge provided by these structures or a hydrodynamically mediated increase in local food availability (Thistle & Eckman, 1990b).

In the coral degradation zone, distinctly different assemblages on coral fragments and in underlying sediment do not seem to occur. There are only slight differences at the family level with Idyanthidae showing a significant preference for the coral fragments. Most of its species are ovoid, slightly depressed and have prehensile first legs, and therefore could be classified as typically 'phytal'. Tetragonicipitidae, known as a characteristic component of every coarse shell-gravel assemblage (Hicks & Coull, 1983), has a higher abundance in the underlying sediment and explains part of the dissimilarity between coral and sediment samples. At the genus level, dissimilarity between the sediment and coral samples was mainly explained by the higher

abundance of *Pseudomesochra*, *Halophytophilus* and *Pseudobradya* on the coral fragments and the higher abundance of *Mesocletodes*, *Leptomesochra* and *Tetragonicipitidae* gen. 1 in the underlying sediment. Preferences were only significant for the genera *Ameiropsis*, *Fultonia*, *Mesochra*, *Idyanthe*, *Haloschizopera* and *Marsteinia* on the coral fragments and for *Xylora* in the underlying sediment. Although certain taxa might show a preference to occur as epifauna, typical interstitial forms of fine to medium sands (Paramesochridae, vermiform Ectinosomatidae, vermiform Ameiridae) (Hicks & Coull, 1983) occur on each of the different microhabitats with similar relative abundances or are too rare to infer significant preferences. The sediment retained between the branches of the coral fragments and on the sponge skeletons might harbour typical sediment-dwellers, and therefore obscure the presence of true epifaunal taxa. Also, species-specific differences in active migration/swimming capabilities are known to occur among sediment-dwelling (Palmer, 1984; Thistle *et al.*, 1995) and phytal meiofauna (Walters & Bell, 1994). Epibenthic species, with their ability to swim, might be expected to perceive the habitat as more fine-grained (*sensu* Jumars, 1975), be less restricted to a particular microhabitat, and thus less aggregated or occur in aggregation of a larger spatial scale (Hicks & Coull, 1983). For example, certain species of the Ectinosomatidae (the most abundant family in the coral degradation zone) are morphologically adapted to emergence and this behaviour might be particularly common in this family (Thistle & Sedlacek 2004). Moreover, the presence of phytal structures (and in analogy herewith the presence of coral fragments) as an additional source of and sink for emerging copepods increases the complexity of possible linkages between benthic and pelagic environments (Walters & Bell, 1994).

Harpacticoids are generally more concentrated in the surface sediment layers than nematodes (Hicks & Coull, 1983). Vincx *et al.* (1994) found copepods in the Porcupine Seabight to exhibit superficial profiles. At 1340 m, around 90% of the copepods and nauplii occurred in the surface centimetre of the sediment. Oxygen tension and food supply are important factors in determining the vertical distribution of meiofauna within the sediment, especially in the deep sea (Vanreusel *et al.*, 1995). Dissolved oxygen decreases most steeply in the upper sediment layers (see Giere, 1993), and copepods are more sensitive to anoxia than nematodes (Moodley *et al.*, 1997). Vincx *et al.* (1994) also suggested a behavioural response in which copepods adopt a more epibenthic lifestyle in the presence of an increased food supply, whereas the nematodes may be better adapted to exploit increased food resources deeper in the sediment. In the deep sea of the SE Pacific Ocean, Ahnert & Schriever (2001) found on average about 87% of the harpacticoids in the top 2 cm of the sediment, with Argestidae, Paramesochridae, Tisbidae, Diosaccidae and Cletodidae as the most surface-associated families and Thalestridae, Paranannopidae, Canthocamptidae and Huntemanniidae penetrating deeper into the sediment (mean depth > 1.5 cm).

Although vertical profiles were not determined in the coral degradation zone, we can expect that the copepod fauna is concentrated in the upper sediment layer. Both overlying biogenic

substrates are physically closely connected to the surface sediment and this may permit considerable exchange between the microhabitats.

3.5.2. Comparison with the sediment-dwelling background community

The family composition of the coral degradation zone is different from both locations with coral-free sediments, as shown by similarity analysis. This is mainly attributed to a higher abundance of Miraciidae, Ameiridae and Pseudotachidiidae in the coral degradation zone and a higher abundance of Huntemanniidae, Cletodidae and Zosimidae at the coral-free locations. Paramesochridae had a significant preference for coral-free sediments, while Pseudotachidiidae showed a preference for the coral degradation zone. However, comparison is limited because of the low number of individuals sampled from the coral-free sediments. Also, differences in depth, geographical position and differences in sediment texture undoubtedly influence the patterns observed.

In the coral degradation zone, the most abundant families are Ectinosomatidae, Ameiridae, Pseudotachidiidae, Argestidae and Miraciidae (in order of decreasing abundance). This corresponds remarkably well with the most abundant of the 19 families reported from two abyssal, muddy sites in the Angola Basin (from a water depth of about 5400 m), being Pseudotachidiidae, Argestidae, Ameiridae, Ectinosomatidae and Neobradyidae (Rose *et al.*, 2005). In the present study, the assignment of species to genera and families is in accordance with recent literature as is the case in Rose et al. (2005) (although they treated *Parameiropsis* as not belonging to Ameiridae). Therefore, faunal compositions of both studies can be compared however with some limitations as study areas differ distinctly both horizontally and vertically. Vincx *et al.* (1994) reported the assemblages in the northeastern Atlantic deep sea as dominated by Cletodidae, Diosaccidae, Ectinosomatidae, Tisbidae and Cerviniidae. However, at the time, certain genera were assigned to different families. For example, several genera, formerly assigned to Cletodidae, now belong to different families (Argestidae, Canthocamptidae, Huntemannidae and Pseudotachidiidae). Also, Tisbidae *sensu* Seifried (2003) now are extremely rare in the deep-sea benthos (Seifried, 2004). The same caution is recommended when comparing with other studies. Ahnert & Schriever (2001) reported Ameiridae, Ectinosomatidae, Argestidae, Tisbidae (majority of the specimens belonging to *Zosime* and *Pseudozosime*) and Neobradyidae as the dominant families in the deep sea of the SE Pacific ocean. In Sagami Bay (central Japan, at 1430 m depth), Miraciidae, Ectinosomatidae, Ameiridae and Tisbidae (with species of *Idyellopsis* and *Zosime*, which now belong to Idyanthidae and Zosimidae, respectively) were the most abundant of the 13 harpacticoid families observed (Shimanaga *et al.*, 2004).

At least at the family level, the copepod fauna in the Porcupine Seabight does not seem to differ markedly from other deep-sea studies in which essentially the same families are dominant. Certain genera, such as *Zosime*, *Pseudomesochra*, *Malacopsyllus*, *Eurycletodes*, *Mesocletodes* and others, are typically found in any deep-sea study (Hicks & Coull, 1983) and are also present in the Porcupine Seabight. While other families, genera and species do occur, detailed comparison at genus or even

species level is however restricted as no complete diversity analysis has been made of northeast Atlantic copepod communities (Vincx *et al.*, 1994). The study of deep-sea harpacticoids from the Great Meteor Seamount (which reaches to about 270 m of water depth) by George & Schminke (2002) is at present the most closely situated study area, located west of the Canary Islands in the subtropical North Atlantic. George & Schminke (2002) detected 28 supraspecific taxa with Paramesochridae, Ectinosomatidae, Diosaccidae and Tisbidae as the most abundant. Of the 11 suprageneric taxa, which were analysed at the species level, Argestidae was found to be the most species-rich with seven genera and 40 species (in the PSB, the family consists of six genera and 18 species). Most of the suprageneric taxa from the Great Meteor Seamount were also present at the PSB, apart from Canuellidae, Cerviniidae, Cylindropsyllinae, Leptastacidae, Leptopontiidae and Styracothoracidae.

The family Ectinosomatidae appears to be an abundant family in deep-sea studies (Seifried, 2004) and, at least in the PSB, it is also the most species-rich family. The few deep-sea studies, conducted at infrafamilial level, report ectinosomatid species as belonging mostly to *Bradya*, *Pseudobradya*, *Ectinosoma* and *Halectinosoma* (e.g. Martínez Arbizu *et al.*, 1998b; Shimanaga *et al.*, 2004). In the PSB, 12 ectinosomatid genera were identified, four of which are characterised by a pair of prehensile first legs (i.e. *Bradyellopsis*, *Halophytophilus*, *Klieosoma* and *Peltobradya*). Known species of *Bradyellopsis*, *Halophytophilus* and *Klieosoma* are mostly reported from the washings of littoral algae, suggesting a shift to hyperbenthic algal biotopes from the sedimentary benthic substrates more typical of the Ectinosomatidae (Noodt, 1971; Hicks & Coull, 1983; Watkins, 1987). However, the relationship between first leg structure and habitat is not so clear (Watkins, 1987), as *Halophytophilus* is also reported from sublittoral sedimentary habitats (Lang, 1948). Harpacticoids exhibit an obvious and enormous variety of morphological forms as adaptations to special conditions in the various habitats (Remane, 1952; Noodt, 1971). Body shape reveals information regarding habitat type and it has been repeatedly noticed that phytal associates generally possess a modified P1 which is strongly prehensile (Bell *et al.*, 1987). The prehensile maxillipeds and first legs are used efficiently as grappling hooks to seize fine microhabitat structures and maintain contact with seaweeds (Hicks, 1985). Certain taxa of the coral degradation zone have a morphology which appears to be typically 'phytal' (such as *Lobopleura*, *Peltobradya* (depressed); *Idyanthe*, *Idyella* (fusiform depressed)) and some of the identified species (*Klieosoma triarticulatum*, *Laophontodes mourois*, *Mesochra pygmaea*, *Laophonte elongata*) have even been reported from the washings of macroalgae (Arroyo *et al.*, 2003; Hicks & Schriever, 1985; Lang, 1948).

The hard biogenic substrates of the coral degradation zone seem to provide a habitat suitable for these typical 'phytal' taxa. However, knowledge of the harpacticoid fauna in the NE Atlantic is at present too limited to assess whether regional diversity is increased substantially by the presence of these complex habitat-providing substrates. For macrofauna, it has been shown in the Porcupine Seabight (at 1000 to 1300 m water depth) that abundance is enhanced and

taxonomic composition is modified by the presence of sponges and the spicule mats derived from them (Bett & Rice, 1992). Furthermore, both corals and sponges have numerous associated organisms (Barthel & Gutt, 1992; Jensen & Frederiksen, 1992; Klitgaard, 1995). However, at least in the NE Atlantic most of the macrofaunal species associated with *Lophelia* seem to be facultative inhabitants representing the fauna present in the local geographical area (Jensen & Frederiksen, 1992; Klitgaard, 1995). This suggests that regional macrofaunal diversity may not be increased substantially by the presence of these large, habitat-creating organisms (Levin *et al.*, 2001). However, regardless of the affinities of the fauna found in *L. pertusa* reefs, it is clear that they harbour a large diversity of associated species (Rogers, 1999). These reefs may act as 'habitat islands' which attract aggregations of species, including many specialist taxa that are rare in the background community (Gage, 1996).

3.5.3. Diversity

Harpacticoids in the deep sea are characterised by high species diversity and low species dominance (Seifried, 2004). At the Quagamire site (at about 1200 m water depth), two species constituted 13% of the harpacticoid fauna (Thistle, 1978). In the Porcupine Seabight, the two most common species each accounted for 5% of the total of adult individuals. The overall ratio of species to individuals (182/901) indicates a different species being encountered in one out of every five individuals.

Rarefaction curves for pooled samples per microhabitat showed no tendency for estimated diversity to reach an asymptote. This suggests that the faunas were characterised not well enough to compare diversity among the microhabitats. Rarefying the samples to a common number of individuals does not eliminate the sensitivity of richness estimates to sampling effort (Levin *et al.*, 2001). Furthermore, Levin *et al.* (2001) warned that although replicates from a site are often pooled, this obscures the actual relationship between number of species and individuals at the sampling scale, and differences in heterogeneity among sites may then contribute to variation in diversity. Therefore, although the rarefaction curves of the pooled data indicate a higher species richness in the underlying sediment, this observation should not be treated as conclusive. Comparison of the different microhabitats, based on separate samples, also is limited due to the small sample sizes of the underlying sediment. Non-parametric tests showed the absence of a significant difference in species richness between sediment and coral fragments. However, in this case the number of species is predicted from the lower portion of the species-individuals curve where the slope is steepest and the error of estimating the number of species is largest (Levin *et al.*, 2001). Generally, all samples of the CDZ are characterised by a high species richness, with sponge skeletons sustaining a slightly lower species richness than coral fragments. Evenness is also equally high in sediment and on the coral fragments, with a slightly higher dominance on the sponge skeletons. However, only two sponge skeletons were sampled and conclusions on this should be considered as provisional.

The biogenic substrata lie relatively unprotected on the sea floor and epifauna could be strongly influenced by current activity, which in the Belgica Mound region is rather high (about 10–25 cm/s) (White, 2006). However, the extent to which the fauna in the underlying sediment is protected from this is unknown. In the deep sea, copepod abundance (Thistle & Levin, 1998) and assemblage structure (Thistle *et al.*, 1999) are known to be affected by current activity, while Thistle (1983a) provided some evidence that differences in hydrodynamics may be less important for copepod diversity. Although the low copepod densities might introduce error in measuring diversity, it seems that the copepod fauna of underlying sediment and coral fragments is equally diverse and does not differ distinctly in terms of evenness. The diversity of nematode assemblages associated with these substrates however appears to be strongly influenced by these hydrodynamical forces. Raes & Vanreusel (2006) showed that the nematode community in the underlying sediment is significantly more diverse than on the coral fragments, because the interstitial habitat is more suitable for nematodes. However, although fewer nematode genera are able to live in the disturbed microhabitat of the coral fragments, the community is not merely dominated by the best adapted ones and evenness in both microhabitats is equally high (Raes & Vanreusel, 2006).

An important characteristic of the deep-sea benthos is that species diversity of many faunal groups increases with depth below the continental shelf (>200 m) to a maximum at mid to lower bathyal depths, and then decreases again with increasing distance seaward on the abyssal plain (>4000 m) (e.g. Gage & Tyler, 1991). Rex (1981) showed that species richness peaks at upper rise depths of around 2000-3000 m for the main mega- and macrofaunal groups including crustaceans (cumaceans). Meiofaunal assemblages also show parabolic patterns of diversity with peaks shifting to even greater depths (Boucher & Lambshead, 1995). In the western North Atlantic, Coull (1972) found a maximum harpacticoid diversity at 3000 m with decreasing diversity thereafter. Baguley *et al.* (2006) proved this typical unimodal relationship for harpacticoids (in the northern Gulf of Mexico) with a maximum species diversity at 1200 m water depth, with decreasing diversity moving into deeper waters. In the coral degradation zone of PSB, the value of ES(30) (based on pooled data of all samples) is 23.9 which agrees well with values at comparable depths in the northern Gulf of Mexico (Baguley *et al.*, 2006). Comparison however is limited because sampling areas differ markedly not at the least in latitudinal position.

Our study area is located at a depth where a peak in species diversity is expected, but this is not certain since unimodal patterns are not universal (Rex *et al.*, 1997; Stuart *et al.*, 2003). Moreover, the coral degradation zone with its wide range of microhabitats provides a structurally more complex environment than normally encountered in the soft-bottom deep sea. At the moment, it is difficult to assess the influence of this increased habitat complexity on regional species diversity, because studies from nearby soft-bottom locations at comparable depth are not available.

Ameiridae Monard 1927 (part.), Lang 1936

Ameira Boeck 1865 (5 sp. + 1 sp.*)
Ameiropsis Sars 1907 (6 sp.)
Filexilia Conroy-Dalton & Huys 1997 (1 sp.)
Leptomesochra Sars 1911 (2 sp.)
Malacopsyllus Sars 1911 (2 new sp.)
Parameiropsis Becker 1974 (1 new sp.)
Parapseudoleptomesochra Lang 1965 (2 sp.)
Pseudameira Sars 1911 (2 sp.)
Sarsameira Wilson 1924 (2 sp.)
Stenocopia Sars 1907 (3 new sp.)
Ameirinae Lang 1944 (4 sp.)

Ancorabolidae Sars 1909, Lang 1944, Lang 1948

Laophontodes T. Scott 1894
Laophontodes mourois Arroyo, George, Benito & Maldonado 2003
1 new sp.
Lobopleura Conroy-Dalton 2004
Lobopleura expansa (Sars 1908)

Argestidae Por 1986

Argestes Sars 1910 (5 new sp.)
Bodinia George 2004 (1 new sp.)
Dizahavia Por 1979 (1 new sp.)
Eurycletodes Sars 1909 (Subgenus *Oligocletodes* Lang 1944)
Eurycletodes (*O.*) aff. *similis* (T. Scott 1895)
1 new sp. + 1 new sp.*
Fultonia T. Scott 1902
Fultonia aff. *bougisi* Soyer 1964
1 new sp.
Mesocletodes Sars 1909
Mesocletodes guillei Soyer 1964
Mesocletodes irrasus (T. & A. Scott 1894)
3 new sp.
Argestidae gen. 1 (1 sp.)

Canthocamptidae Sars 1906 (part.), Monard 1927 (part.), Lang 1948

Bathycamptus Huys & Thistle 1989 (3 new sp.)
Mesochra Boeck 1865
Mesochra pygmaea (Claus 1863)
Canthocamptidae gen. 1 (8 sp. + 2 sp.*)

Cletodidae T. Scott 1905 (part.) *sensu* Por 1986

Cletodes Brady 1872 (1 sp. + 2 sp.*)
Enhydrosoma Boeck 1872 (1 sp.)

Ectinosomatidae Sars 1903 (part.), Olofsson 1917

Bradya (Subgenus *Bradya* Lang 1944) (2 sp.)
Bradya (Subgenus *Parabradya* Lang 1944) (2 sp.)
Bradyellopsis Brian 1924 (1 new sp.)
Ectinosoma Boeck 1865 (3 sp. + 1 sp.*)
Halectinosoma Lang 1944 (1 sp. + 1 sp.*)
Halophytophilus Brian 1917 (3 new sp. + 1 new sp.*)
Hastigerella Nicholls 1935 (1 new sp. + 1 new sp.*)

Klieosoma Hicks & Schriever 1985
Klieosoma triarticulatum (Klie 1949)
2 new sp.
Lineosoma Wells 1965 (1 new sp. + 1 new sp.*)
Microsetella Brady & Robertson 1873
Microsetella norvegica (Boeck 1865)
Peltobradya Médioni & Soyer 1967 (1 new sp.)
Pseudobradya Sars 1904 (7 sp. + 1 sp.*)
Sigmatidium Giesbrecht 1881 (7 sp. + 1 sp.*)
Ectinosomatidae gen. 1 (3 sp.)

Harpacticidae Sars 1904
Perissocope Brady 1910 (1 new sp.)

Huntemanniidae Por 1986
Metahuntemannia Smirnov 1946 (2 new sp.)
Talpina Dahms & Pottek 1992 (1 new sp.*)

Idyanthidae Lang 1944
Idyanthe Sars 1909
Idyanthe dilatata (Sars 1905)
4 new sp.
Idyella Sars 1906
Idyella major Sars 1920
1 new sp.
Nematovorax Bröhldick 2005
Nematovorax gebkelinae Bröhldick 2005
Idyanthidae gen. 1 (2 new sp.)

Laophontidae T. Scott 1905
Archesola Huys & Lee 2000 (1 new sp.)
Heterolaophonte Lang 1944 (1 new sp.)
Laophonte Philippi 1840
Laophonte elongata Boeck 1872
3 new sp.

Miraciidae Dana 1846
Amphiascus Sars 1905 (2 sp. + 1 sp.*)
Amphiascoides Nicholls 1941 (1 sp.)
Haloschizopera Lang 1944 (1 sp.)
Rhyncholagena Lang 1944 (1 sp.)
Robertgurneya Lang 1944 (1 sp.*)

Neobradyidae Olofsson 1917
Marsteinia Drzycimski 1968 (3 new sp.)
Neobradyidae gen. 1 (1 new sp.)

Normanellidae Lang 1944 *sensu* Huys & Willems 1989
Sagamiella Lee & Huys 1999 (1 new sp.*)

Novocriniidae Huys & Iliffe 1998
Atergopedia Martínez Arbizu & Moura 1998
Atergopedia vetusta Martínez Arbizu & Moura 1998
Novocriniidae gen. 1 (1 new sp.)

Paramesochridae Lang 1944
Diarthrodella Klie 1949
Diarthrodella aff. *orbiculata* Klie 1949
Kliopsyllus Kunz 1962 (2 new sp.*)

Leptopsyllus T. Scott 1894 (1 new sp. + 1 new sp.*)
Paramesochra T. Scott 1892 (4 new sp. + 1 new sp.*)
Scottopsyllus Kunz 1962 (Subgenus *Scottopsyllus* Kunz 1962)
Scottopsyllus (*Sc.*) aff. *robertsoni* (T. & A. Scott 1895)
Paramesochridae gen. 1 (1 sp.*)

Pseudotachidiidae Lang 1936
Cylindronannopus Coull 1973 (1 new sp.)
Idomene (?) Philippi 1843 (2 sp.)
Pseudomesochra T. Scott 1902 (7 new sp.)
Xylora Hicks 1988 (2 new sp.)
Pseudotachidiidae gen. 1 (1 sp.)

Rhynchothalestridae Lang 1948
Rhynchothalestris Sars 1905 (1 new sp.)

Tegastidae Sars 1904
Tegastes Norman 1903 (1 sp.)

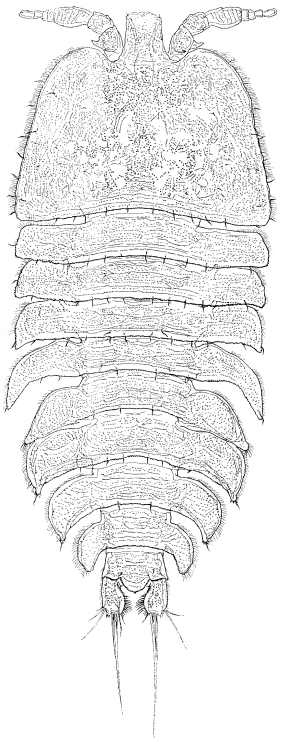
Tetragonicipitidae Lang 1944
Tetragonicipitidae new gen. (1 new sp.)

Zosimidae Seifried 2003
Zosime Boeck 1872
Zosime bergensis Drzycimski 1968
Zosime paramajor Bodin 1968
Zosime aff. *pacifica* Fiers 1991*
1 new sp.*

Appendix. List of identified families, genera and species from the Porcupine Seabight (*: exclusively present in coral-free sediment).

CHAPTER 4

Peltidiphonte gen. n., a new taxon of Laophontidae (Copepoda: Harpacticoida) from coral substrates of the Indo-West Pacific Ocean



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from coral substrates of the Indo-West Pacific Ocean.
Hydrobiologia 553: 171-199.

4.1. ABSTRACT

A new genus of the harpacticoid family Laophontidae is described and named *Peltidiphonte* gen. n. Eight new species are assigned to this genus; they were collected from different locations in the Indo-West Pacific Ocean, including the Comoros, the Kenyan coast, the Red Sea, the Andaman Islands, the northern coast of Papua New Guinea, the Solomon Islands and the northeastern coast of Australia. Most of the specimens were collected from dead coral substrates, suggesting a close affinity between the members of the new genus and this substrate. *Peltidiphonte* gen. n. can easily be discriminated from other genera of the family by the extremely depressed body and by the shape of the antennule, bearing two (or three) processes on the first segment and a hook-like process along the outer margin of the second segment. An identification key for the new genus is provided.

Keywords: Copepoda, Harpacticoida, Laophontidae, *Peltidiphonte* gen. n., Indo-West Pacific, dead coral substrates.

4.2. INTRODUCTION

Harpacticoid copepods show a high level of habitat specificity and adaptation to their environment (Hicks & Coull, 1983; Huys & Boxshall, 1991), resulting in a high diversity of body forms as classified by Noodt (1971) and Coull (1977). The speciose family of Laophontidae comprises a large number of these body forms, including fusiform prehensile (e.g. *Esola* Edwards, 1891), cylindrical (e.g. *Wellsiphontina* Fiers, 1991), vermiform (e.g. *Afrolaophonte* Chappuis, 1960) and compressed (e.g. *Robustunguis* Fiers, 1992). This variety in body shapes reflects differences in ecology and (micro)habitat preference within the Laophontidae (e.g. epibenthic, interstitial) (Hicks & Coull, 1983).

Meiobenthos samples from dead coral substrates yielded several new species of Laophontidae which belong to an unknown genus. Within the Laophontidae, the newly established genus is well defined by its conspicuous, dorso-ventrally flattened body form.

4.3. MATERIAL AND METHODS

During intensive sampling campaigns in the Indo-West Pacific Ocean (Andaman Islands: 1983; Australia: 1984; Comoros: 1981, 1985; Kenya: 2002; Papua New Guinea: 1977, 1978, 1979, 1981, 1982; Red Sea: 1983, 1986; Solomon Islands: 1982), meiofauna samples were collected from various dead coral substrates (ranging from coral sand, fine coral gravel and coral rubble to large coral fragments). All samples were taken in the tidal and subtidal zone down to a depth of 84 m. Epifauna from coral fragments and coral rubble were rinsed off over a 1 mm and a 38 μm sieve. Samples from coral gravel were obtained by decanting the coral gravel (ten times) over a 38 μm sieve. Shortly after collection, buffered formaldehyde was added to a final concentration of 4%.

In the laboratory, samples were rinsed over a 1 mm sieve with a jet of freshwater, then decanted ten times over a 38 μm sieve, centrifuged three times with Ludox HS40 (specific density 1.18), and finally stained with Rose Bengal. Meiofauna was sorted and counted at the higher taxon level using a Wild M5 binocular. Harpacticoid copepods were stored in 75% ethanol.

Dissected parts of the specimens were mounted in glycerine. Preparations were sealed with insulating varnish. Observations and drawings were made on a light microscope (Leica DM LS) equipped with a drawing tube. In toto specimens are stored in 75% neutralised ethanol. Type specimens are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, labelled COP). Scale bars in figures are indicated in μm.

The descriptive terminology of Huys *et al.* (1996) is adopted. Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus.

4.4. SYSTEMATICS

Family **Laophontidae T. Scott, 1905**

Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**

Genus ***Peltidiphonte* Gheerardyn & Fiers gen. n.**

Diagnosis

Laophontidae. Body depressed to strongly depressed. Cephalothorax flattened. Free prosomites with laterally extended, winglike pleurotergites; first urosomite with backwardly produced wings; urosomites (except anal somite) broad and winged, backwardly produced. Free prosomites as wide as cephalothorax, urosomites tapering posteriorly. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation; fused ventrally. Male urosome more slender than in female urosome, with a transversal row of long spinules on the ventral surface of the third urosomite. Cephalothorax and body somites with smooth, indistinctly or distinctly serrate posterior margin. Integument of the cephalothorax partly pitted and partly covered with small denticles, or entirely pitted; integument of the prosomites and urosomites pitted, covered with small denticles, with combs of small denticles or with a combination of these structures. Rostrum fused to cephalothorax, variable in shape but always large, prominent and dorsally pitted. Anal operculum convex and more or less backwardly produced.

Antennule 6- or 7-segmented in ♀, sub-chirocer and 8-segmented in ♂; aesthetascs on segment 4 and most distal segment in ♀ and on segments 5 and 8 in ♂; segment 1 with a blunt process proximally on the dorsal surface and with a blunt or sharp, small to large process along the outer margin, with or without an additional uneven process in between; segment 2 with an outer thorn-like process variable in size (small thorn to large posteriorly directed hook). Antennary exopod well-developed with 3 pinnate setae and 1 subdistal, short and naked seta. Mandibular palp small, uniramous with 1, 1, 3 setae, representing basis, exopod and endopod,

respectively. Maxillule with 1 pinnate seta and 1 naked seta on coxa; basis with 1 pinnate and 2 naked seta(e); endopod represented by 3 setae; exopod with 2 setae. Maxillary syncoxa with 2 endites, lacking praecoxal one; proximal endite with comb-like claw and 1 seta; distal endite with 3 setae; endopod represented by a single seta. Maxilliped with 2 pinnate setae on syncoxa; endopodal claw unarmed, with 1 short seta at base.

Swimming legs P1-P4 with 3-segmented exopods and 2-segmented endopods; chaetotaxy of third exopodal segments of P2-P4: 123, 223 and 223, respectively. Swimming leg setal formulae in Table 1. Male endopodites with setal formula as in ♀, without apophysis in P3. Male exopodal segments of P3 and P4 only in two species (*Peltidiphonte maior* sp. n. en *P. paracristata* sp. n.) more robust than in female. P5 with separate exopod and baseoendopod. Exopod reaching far beyond the baseoendopod, ovate to elongate in ♀, rectangular in ♂ and bearing 5 plumose setae. Endopodal lobe of female P5 with 4 elements: 2 strong and unipinnate spines proximally, and 2 plumose setae sub-apically and apically. Male baseoendopod rudimentary with 1 seta. P6 vestiges bearing 1 seta in ♀; vestiges asymmetrical in ♂, with outer distal corner produced into cylindrical process bearing 2 setae.

Caudal rami either cylindrical, or with bulbous inner margin; seta I-II-III closely set, all naked; setae IV-V not fused.

Type species – *Peltidiphonte rostrata* Gheerardyn & Fiers gen. n., sp. n.
Other species – *P. andamanica* Gheerardyn & Fiers sp. n.; *P. cristata* Gheerardyn & Fiers sp. n.; *P. furcata* Gheerardyn & Fiers sp. n.; *P. maior* Gheerardyn & Fiers sp. n.; *P. morovoensis* Gheerardyn & Fiers sp. n.; *P. ovata* Gheerardyn & Fiers sp. n.; *P. paracristata* Gheerardyn & Fiers sp. n.
Etymology – The generic name is a conjunction of Peltidiidae and the suffix *-phonte* and refers to the depressed body shape resembling the habitus of the harpacticoid family Peltidiidae. Gender: feminine.

	P2	P3	P4
Peltidiphonte cristata	0.1.123 0.220	0.1.223 0.220	0.1.223 0.121
Peltidiphonte maior	0.1.123 0.220*	0.1.223 0.220	0.1.223 0.121
Peltidiphonte ovata	0.1.123 0.220	0.1.223 0.220	0.1.223 0.121
Peltidiphonte paracristata	0.1.123 0.220	0.1.223 0.220	0.1.223 0.121
Peltidiphonte rostrata	0.1.123 0.220	0.1.223 0.120	0.1.223 0.120
Peltidiphonte furcata	0.1.123 0.120	0.1.223 0.120	0.1.223 0.120
Peltidiphonte morovoensis	0.1.123 0.120	0.1.223 0.120	0.1.223 0.120
Peltidiphonte andamanica	0.1.123 0.120	0.1.223 0.110	0.1.223 0.110

Table 1. Species of *Peltidiphonte* gen. n. Swimming leg setal formulae
(*: specimens with 0.120 are not rare.)

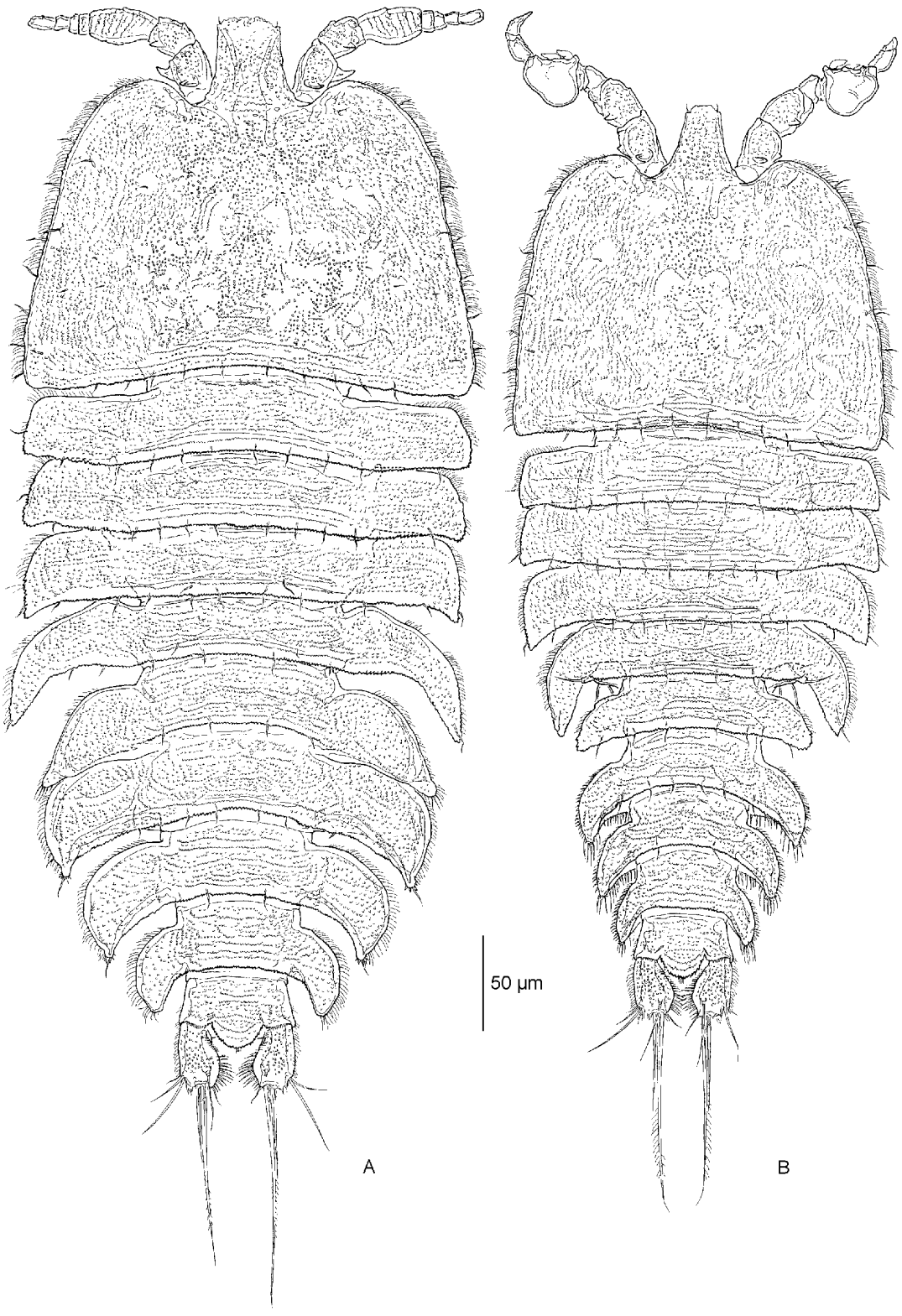

Figure 1. *Peltidiphonte rostrata* sp. n. (A) female habitus, dorsal; (B) male habitus, dorsal.

***Peltidiphonte rostrata* Gheerardyn & Fiers gen. n., sp. n.** (Figures 1-5)

Type locality – Western Indian Ocean, Kenyan coast, in front of village Kanamai (3° 55' S, 39° 47' E), collected from dead coral fragments, water depth less than 0.5 m.
Material – (a) From type locality: holotype ♀ on 1 slide (COP 4690); allotype ♂ on 1 slide (COP 4691); paratypes are 2 ♀♀ and 7 ♂♂ dissected on slides (COP 4692 – COP 4700), and 4 ♀♀ and 12 ♂♂ (COP 4701) and 24 ♀♀, 16 ♂♂, 3 CII, 5 CIII, 7 CIV and 3 CV (COP 4702) preserved in 70% alcohol; all collected 21 February 2002.

(b) Western Pacific Ocean, Papua New Guinea, different locations in Madang Province [Laing Island (4° 11' S, 144° 52' E), Hansa Bay (Duangit Reef) (4° 10' S, 144° 53' E), Chirimosh Island (4° 23' S, 145° 14' E), Megiar Harbour (4° 49' S, 145° 46' E)], coral sand and dead coral fragments, in tidal pools and the subtidal zone to a water depth of 46 m. – paratypes are 4 ♀♀ and 3 ♂♂ dissected on slides (COP 4703 – COP 4709), and numerous ♀♀ and ♂♂ (COP 3092), 8 ♀♀ and 6 ♂♂ (COP 4711), 8 ♀♀ and 5 ♂♂ (COP 4712), 3 ♀♀ and 4 ♂♂ (COP 4713) and 4 ♀♀ (COP 4710) preserved in 70% alcohol; collected in June 1977, May 1979 and July 1981.
Etymology – The species name refers to the conspicuous, truncated rostrum.

Description of female

Total body length 508 – 585 μm (n = 10; average = 547 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 232 μm.

Rostrum (Fig. 2A) slightly longer than broad, with parallel margins and truncated at the tip; continuous with cephalothorax; with a pair of sensillae anteriorly; dorsal surface pitted; margin at the tip serrated.

Habitus (Fig. 1A). Body strongly depressed. Largest width near the posterior margin of the cephalothorax. Cephalothorax flattened, slightly broadening posteriorly. Free prosomites as wide as cephalothorax; urosome tapering posteriorly. First urosomite with posteriorly extended wings; following urosomites (except anal somite) broad and winged, posteriorly extended. Second and third urosomite fused to form genital double-somite. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation; fused ventrally.

Integument of the cephalothorax medially pitted and laterally with small denticles; having medially a symmetrical pattern of smooth areas; regularly ornamented with small sensillae. Posterodorsal margins of cephalothorax and somites serrate. Surface of pleurotergites with a pattern of transversally arranged small denticles. Anal somite bearing dorsally small denticles and some pits. Anal operculum crescentic with serrate margin and flanked by 2 sensillae. Caudal rami pitted dorsally.

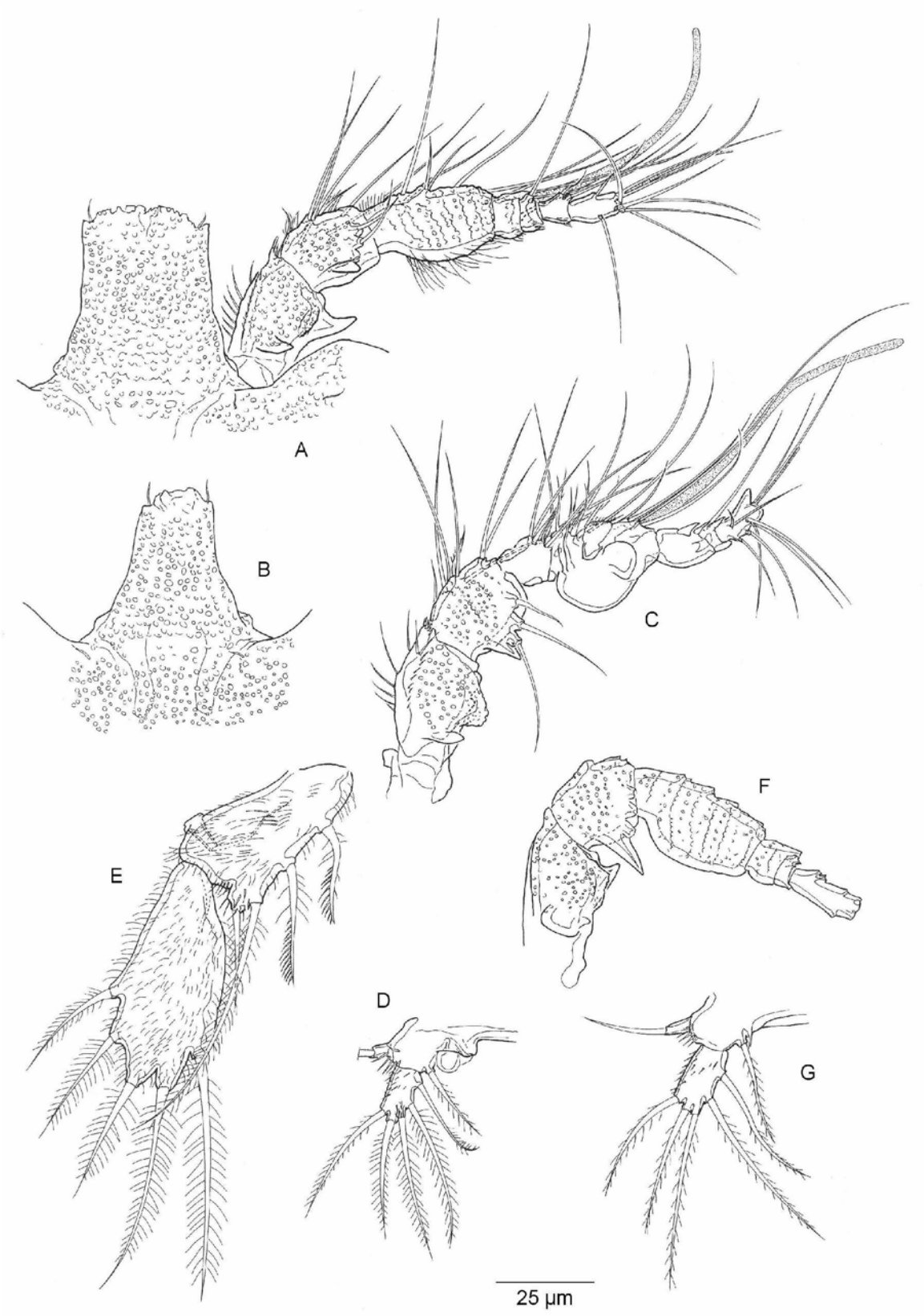

Figure 2. *Peltidiphonte rostrata* sp. n. (A) female rostrum and antennule, dorsal; (B) male rostrum, dorsal; (C) male antennule, dorsal; (D) male P5, anterior; (E) female P5, anterior; (F) female antennule (paratype, armature omitted), dorsal; (G) male P5 (paratype), anterior.

Posterodorsal margins of cephalothorax and free somites (except penultimate urosomite) bearing a number of small sensillae of which the number decreases posteriorly.

Ventral surface (Fig. 5D) of the genital double-somite smooth, except for some median striae; of the following two urosomites smooth. Ventral surface of anal somite hairy laterally and smooth medially. Ventral surface of caudal rami hairy. Posteroventral margin of genital double-somite smooth medially, hairy along some distance of lateral side; posteroventral margins of following two urosomites with a row of strong spinules medially and hairy along the lateral sides.

Caudal rami (Fig. 5B) 1.6 times as long as wide; having a convex inner and a straight outer margin; several spinular rows ventrally and along inner margin. Setae I, II and III inserted in distal fourth of outer margin; seta I naked, shortest; setae II and III naked; setae IV and V both pinnate; seta VI naked and small; seta VII implanted in the distal fourth.

Antennule (Fig. 2A) seven-segmented; outwardly directed; majority of setae long and slender; segment 1 to 4 dorsally pitted and with small denticles, ventrally smooth; segment 5 to 7 smooth. Segment 1 dorsally with blunt thorn on proximal half; the outer margin bearing a rather large thorn, with an uneven process dorsally from it; spinular rows along inner and distal margin. Segment 2 with an outer small thorn. Segment 3 longest; outer margin convex and densely covered with fine spinules. Armature formula: I-1, II-9, III-7, IV-2 + ae, V-1, VI-2, VII-9 + ae.

Antenna (Fig. 3F). Coxa with cluster of spinules on abexopodal side. Allobasis with 1 short and unipinnate abexopodal seta. Exp unisegmented with 3 sub-equal pinnate setae and 1 subdistal, short and naked seta. Enp with 2 rows of spinules and 2 subapical frills; with following armature: subapically 2 spines and a slender seta, apically 1 long robust spine, 1 small clawlike spine, 3 geniculate setae (the outermost pinnate) and 1 slender seta.

Mandible (Fig. 3A, 3B). Gnathobase well developed. Biting edge formed by several blunt teeth and a seta. Surface smooth, except for some spinules along the outermost margin. Palp uniramous; endopod and exopod represented by 3 and 1 smooth seta(e), respectively. Medial seta plumose.

Maxillule (Fig. 3C). Praecoxa with a rather slender arthrite; bearing a row of long spinules on posterior surface of arthrite; medial margin furnished with 8 spines. Coxal endite with 1 pinnate seta and 1 slender naked seta. Basal endite with 3 setae (1 pinnate, 2 bare). Endopod obsolete, represented by 3 setae. Exopod 1-segmented with 2 apical setae.

Maxilla (Fig. 3D). Syncoxa with a row of long spinules along distal outer edge and 2 rows of small spinules on posterior surface; with 2 endites. Proximal endite with comb-like claw and 1 seta; distal one with 3 setae. Allobasis drawn out into strong, slightly curved, distally pinnate claw with 2 setae. Endopod obsolete, represented by a single seta.

Maxilliped (Fig. 3E). Syncoxa with 2 pinnate setae and two or three rows of spinules. Basis with 2 to 3 spinules on outer margin. Endopod clawshaped, unarmed, with short naked seta at base.

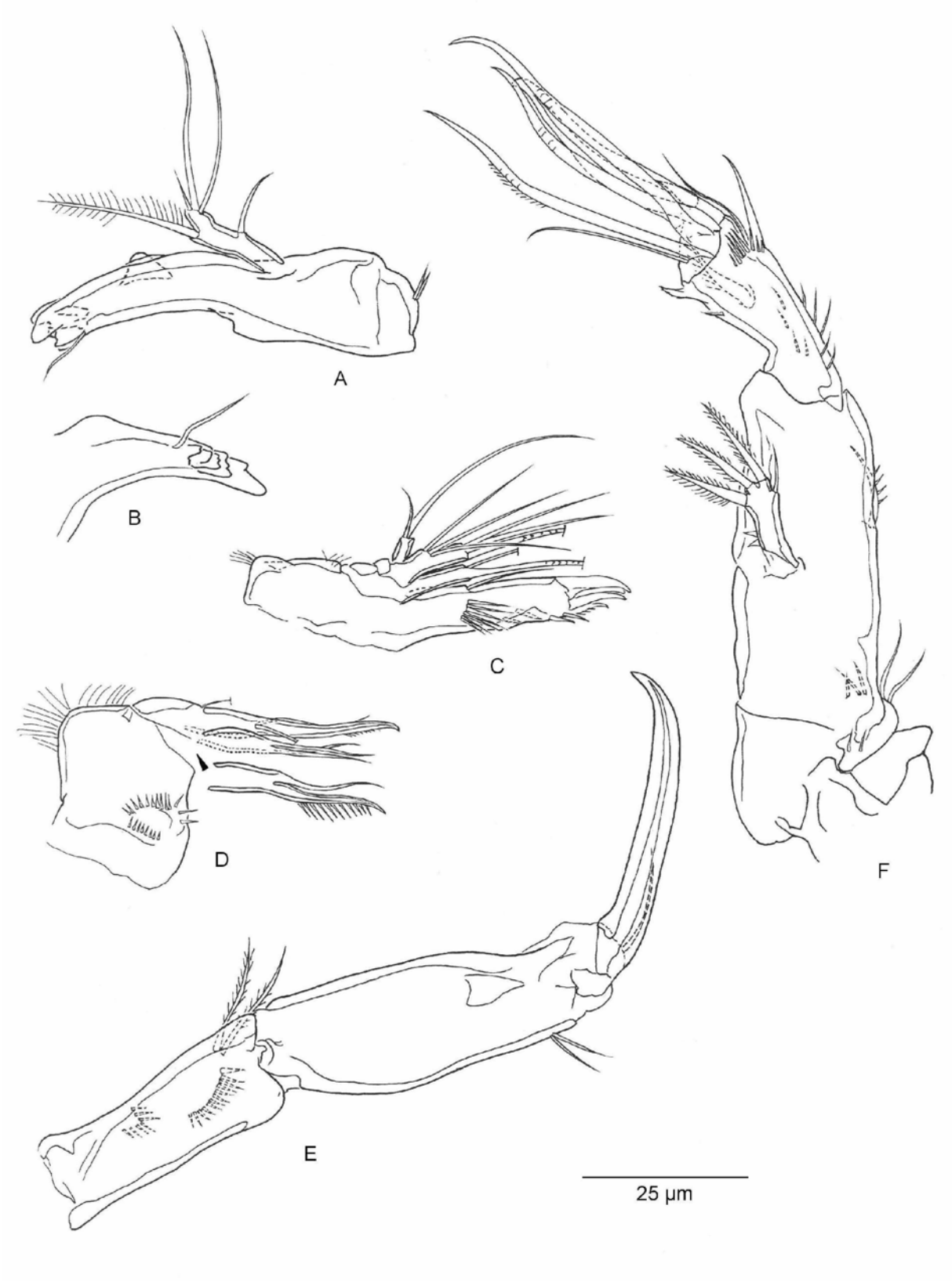

Figure 3. *Peltidiphonte rostrata* sp. n. (A,B) mandible; (C) maxillule; (D) maxilla (arrow indicating original position of proximal endite); (E) maxilliped; (F) antenna.

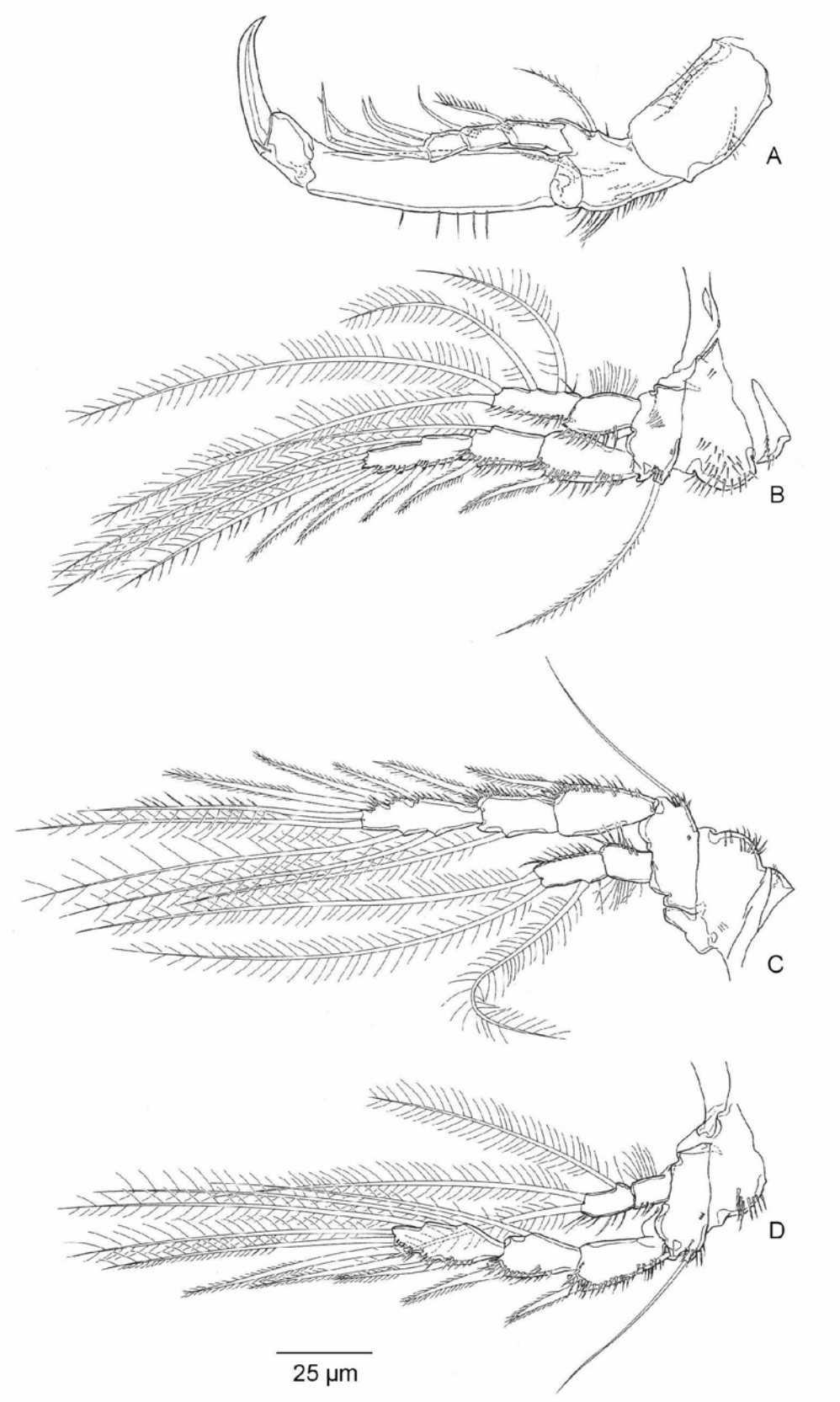

Figure 4. *Peltidiphonte rostrata* sp. n. (A) female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior.

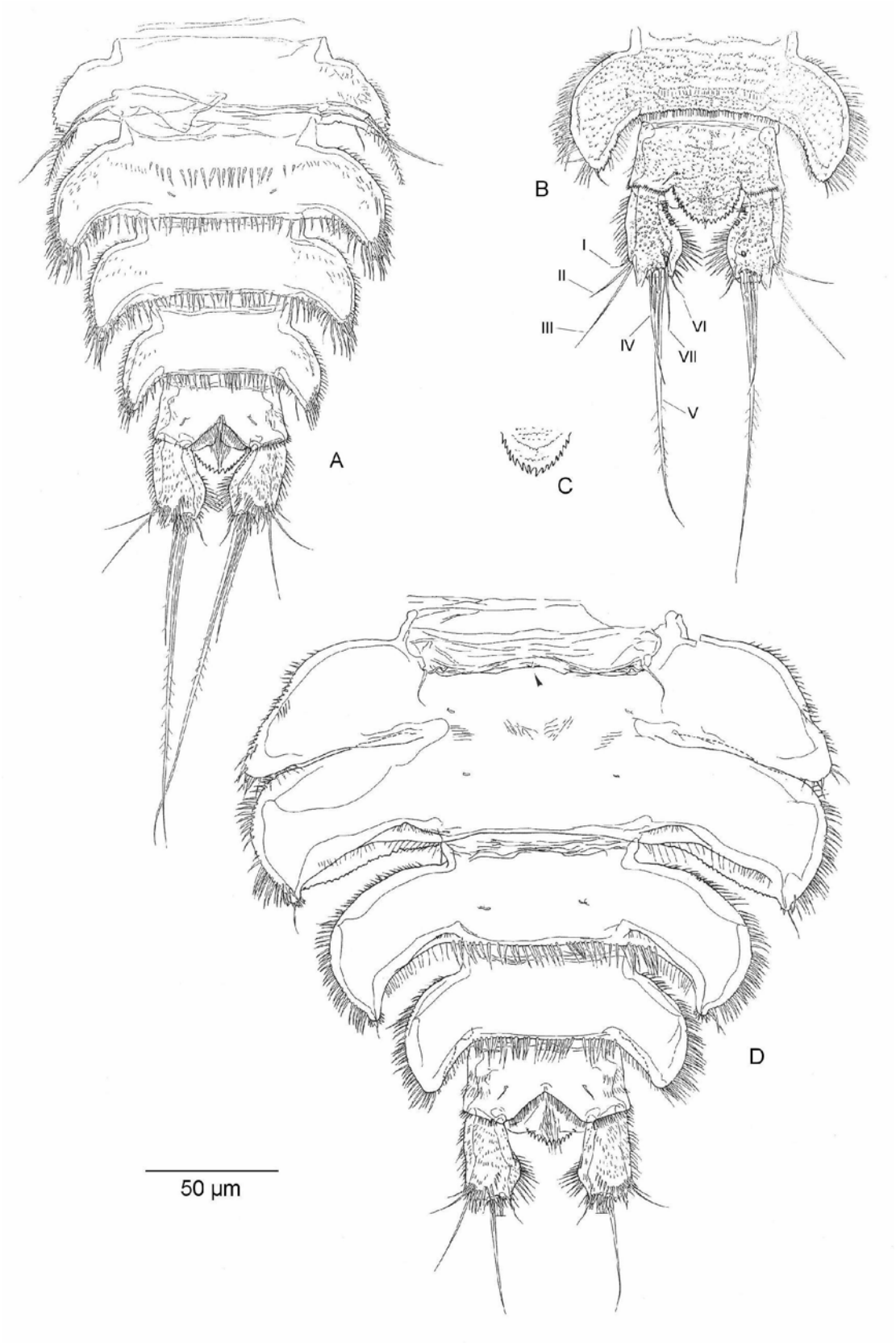

Figure 5. *Peltidiphonte rostrata* sp. n. (A) male urosome, ventral ; (B) female anal somite and caudal rami, dorsal; (C) anal operculum (paratype), dorsal; (D) female urosome, ventral (arrow indicating copulatory pore).

P1 (Fig. 4A). Coxa cylindrical with two rows of spinules. Basis with 1 pinnate seta along outer margin; medial seta arising in middle of anterior surface; long spinules on anterior surface, along inner and outer margin; 1 anterior tube pore near articulation with coxa. Exp-1 with 1 unipinnate outer spine; exp-2 with 1 naked outer spine; exp-3 with 2 naked outer spines and two geniculate apical setae. Enp-1 with long spinules along inner margin; enp-2 with 1 strong, smooth claw and 1 minute, naked accessory seta.

P2-P4 (Fig. 4B, 4C, 4D). Setal formula in table 1. Exopodites 3-segmented and endopodites 2-segmented. Prae-coxae triangular with an outer row of small spinules. Coxae with outwards directed spinules on anterior surface. Bases with a spinular row near the insertion place of the basal seta and 1 tube pore on anterior surface. Outer margin of basis with long, slender, pinnate (P2) or naked (P3-P4) seta. Endopodite P2 reaching beyond the middle of the second exopodal segment. Endopodite P3 only slightly longer than the first exopodal segment. Endopodite P4 as long as the first exopodal segment. Segments of endopods and exopods with pattern of spinules as figured.

P5 (Fig. 2E) with separate exopod and baseoendopod; both anteriorly densely covered with spinules as figured. Basal seta arising from a long cylindrical setophore (recurved in illustration). Proximal spines of endopodal lobe strong and armed as figured; sub-apical and apical seta plumose. Exopodite reaching far beyond the baseoendopod; ovate; about 2 times as long as wide; bearing 5 plumose setae, closely set in distal region.

P6 vestiges (Fig. 5D) bearing 1 seta. Copulatory pore minute.

Description of male

Total body length 419 – 494 μm (n = 10; average = 466 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 192 μm.

Rostrum (Fig. 2B) remarkably less wide than in female, tapering towards the tip, but ornamented as in female.

Habitus (Fig. 1B, 5A). Smaller and more slender than female. Second and third urosomite fully separated. Urosome remarkably slender than female urosome. Ventral surface of the third urosomite with a transversal median row of spinules. Posteroventral margins of third to fifth urosomite bearing a row of strong spinules.

Antennule (Fig. 2C) eight-segmented; sub-chirocer. Segment 1 dorsally with blunt thorn on proximal half; bearing along the outer margin a very small, blunt thorn (unlike the female), with an uneven process dorsally from it. Segment 2 as in female. Armature formula: I-1, II-10, III-6, IV-2, V-12 (?) + ae, VI-0, VII-1, VIII-9 + ae.

Mouthparts and P1-P4 as in female.

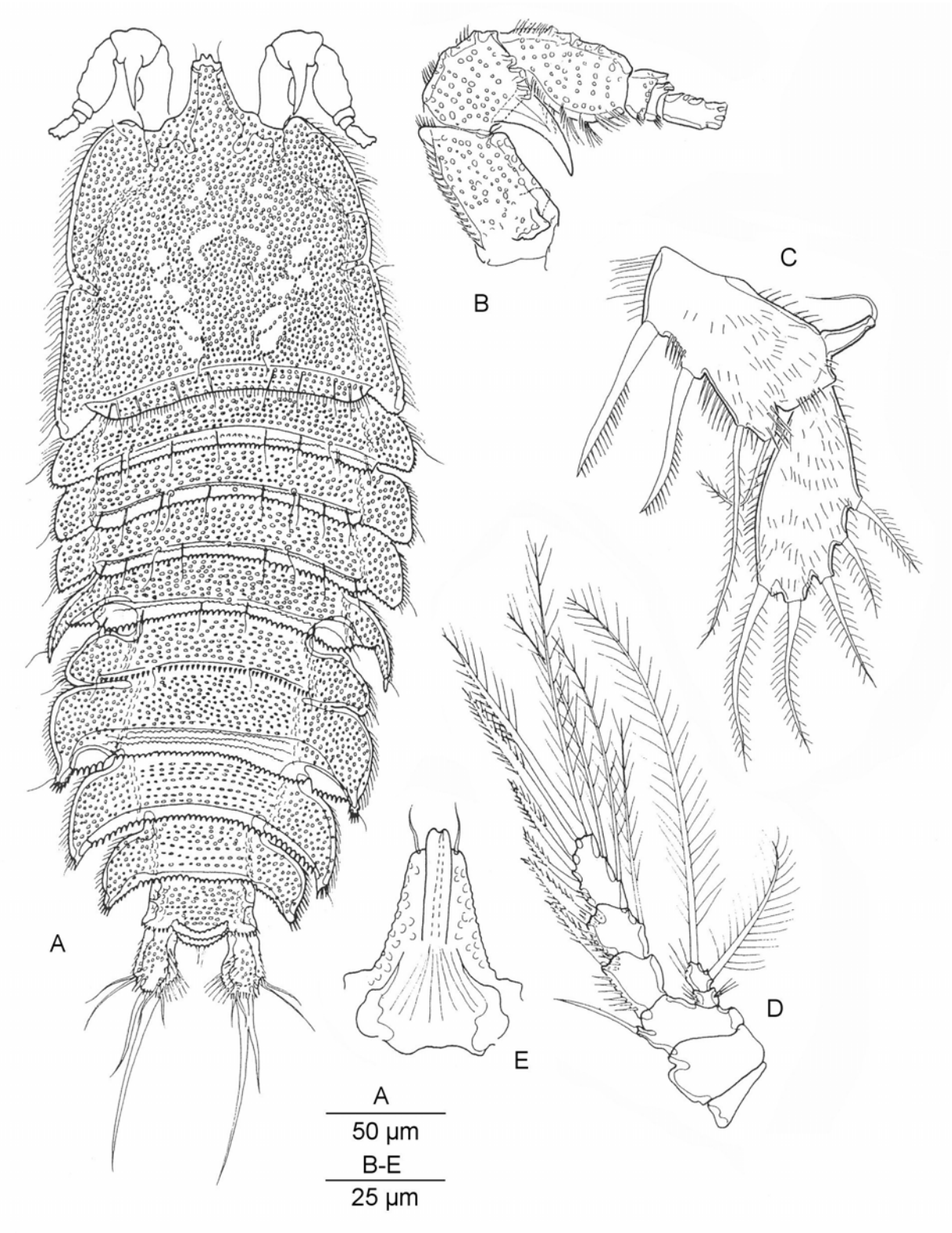

Figure 6. *Peltidiphonte andamanica* sp. n. (A) female habitus, dorsal; (B) female antennule (armature omitted), dorsal; (C) female P5, anterior; (D) female P4, posterior; (E) female rostrum, ventral.

P5 (Fig. 2D). Endopodal lobe of baseoendopod obsolete; bearing one plumose seta with a hyaline structure medially next to it. Basal part with an outer naked seta arising from a setophore. Outer margin bearing some longer spinules. Exopodite oblong; about twice as long as wide, bearing five plumose setae: 1 outer, 1 apical, and 3 inner ones. Outer margin and anterior surface with spinules.

P6 vestiges (Fig. 5A) asymmetrical. One vestige functional; one vestige fused to somite. Both produced into a long cylindrical process bearing a sub-apical inner pinnate and an apical smooth seta.

Variability – Most specimens from Papua New Guinea differ in some aspects from the Kenyan material. The female A1 is 6-segmented (as a result of the fusion of the sixth and seventh segments) and the outer process on segment 2 of A1 is somewhat larger (Fig. 2F). The hyaline structure on the baseoendopod of the male P5 is less developed or absent (Fig. 2G). While the posterolateral angles of the second urosomite of the male are rather rounded in the specimens from Kenya, they are sharpened (comparable to the shape of the first urosomite) in most specimens from Papua New Guinea. Finally, the teeth around the margin of the anal operculum are larger (Fig. 5C). However, the samples from Papua New Guinea included also specimens which did not show any of these differences.

Differential diagnosis – *Peltidiphonte rostrata* is clearly distinguished from the other species of the genus by its conspicuous, truncated rostrum with parallel margins and the rather small process along the outer margin of segment 2 of A1. All other species have a more or less triangular rostrum with a bifid tip and the process along the outer margin of segment 2 of A1 occurs as a large posteriorly directed hook. *P. rostrata* also has a unique setal formula within the genus.

Known range – *P. rostrata* is known from the Kenyan coast (type locality) and the northern coast of Papua New Guinea (Madang Province).

Peltidiphonte andamanica **Gheerardyn & Fiers sp. n.** (Figure 6)

Type locality – Indian Ocean, Andaman Islands, Jolly Boy Island (11° 31' N, 92° 37' E), submerged coral reef, water depth 1 to 1.5 m, coral sand between soft corals.

Material – From type locality: holotype ♀ dissected on 1 slide (COP 2428); collected 5 April 1983.

Etymology – The species name refers to the type locality of this species.

Description of female

Total body length 400 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 150 μm.

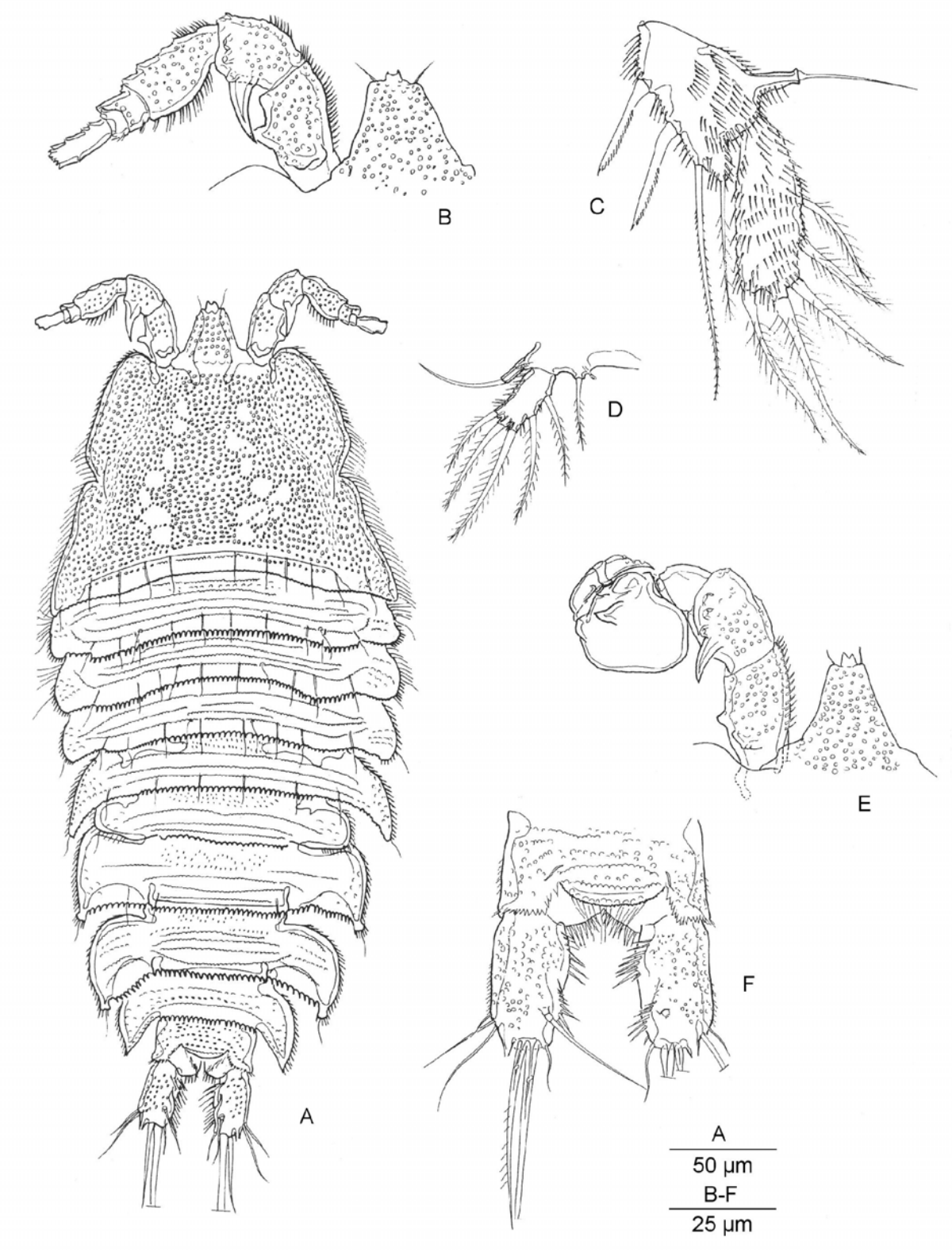

Figure 7. *Peltidiphonte cristata* sp. n. (A) female habitus, dorsal; (B) female rostrum and antennule (armature omitted); (C) female P5, anterior; (D) male P5, anterior; (E) male rostrum and antennule (armature omitted), dorsal; (F) female caudal rami, dorsal.

Rostrum (Fig. 6E) large with straight margins; rather narrow; tapering towards the bifid tip; ventral surface with distinct smooth carina, supporting the tip; integument dorsally and ventrolaterally pitted.

Habitus (Fig. 6A). Body depressed; rather elongated in dorsal view. Cephalothorax tapering slowly towards the front; slightly constricted near the middle. Pleurotergites of prosome with rounded lateral margins. First urosomite with sharp, posteriorly directed wings. Anterior part of genital double-somite somewhat narrower and with rounded margins. Following urosomites (except anal somite) broad and winged; posteriorly extended.

Dorsal integument entirely pitted. Posterodorsal margin of cephalothorax smooth; posterolateral angles lobate with a serrate margin. Posterodorsal margins of prosomites and urosomites (including both urosomites which form the genital double-somite) distinctly serrate over the entire length. Anal operculum with two parallel serrate combs and a serrate margin. Caudal rami pitted dorsally.

Ventral surface of anterior part of the genital double-somite striated. Ventral integument of the following urosomites smooth. Posteroventral margins of genital double-somite and following urosomites spinulose. Caudal rami smooth ventrally.

Caudal rami 1.3 times as long as wide; inner margin strongly convex in the second half, bearing long spinules; outer margin straight; seta I, II, III and VII implanted almost apically.

Antennule (Fig. 6B) six-segmented; segment 1 to 4 dorsally pitted and provided with spinules along their margins; segment 4 and 5 with a wreath of small spinules; segment 6 smooth. Segment 1 dorsally with a blunt thorn on the proximal half; the outer margin bearing a blunt thorn proximally. Segment 2 with an outer large thorn.

Mouthparts and P1-P5 (Fig. 6C, 6D) as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1. Endopods of P2-P4 not reaching beyond the first exopodal segment; all having a compact appearance.

Male unknown.

Differential diagnosis – *Peltidiphonte andamanica* exhibits the most reduced chaetotaxy in the genus. Enp-2 of P3-P4 bear only two setae. The segments of the legs have a compact appearance. The integument of *P. andamanica* is very densely pitted.
Known range – *P. andamanica* is known from the type locality only.

Peltidiphonte cristata **Gheerardyn & Fiers sp. n.** (Figure 7)

Type locality – Western Indian Ocean, Comores Islands, Grande Comore, 1 km north of Moroni (11° 42' S, 43° 14' E), sand sample, water depth 15 m.

Material – (a) From type locality: holotype ♀ dissected on 1 slide (COP 2429); allotype ♂ on 1 slide (COP 4655); paratypes are 1 ♀ and 1 ♂ dissected on slides (COP 4656 – COP 4657) and 19 ♀♀, 6 ♂♂ and 3 CV (COP 2431) preserved in 70% alcohol; all collected 24 November 1985;

(b) Western Indian Ocean, Comoros, different locations on Grande Comore [Foumbouni (11° 51' S, 43° 29' E), Chindini (11° 55' S, 43° 29' E)], sand samples, different water depths (10 m to 30 m). – paratypes are 3 ♂♂ (COP 2432), 1 ♀ and 1 ♀CV (COP 2433), 1 ♀ (COP 2436), 1 ♀ (COP 2437), and 1 ♀ (COP 2438) preserved in 70% alcohol; all collected in August 1981.

Etymology – The species name refers to the transversal combs of small denticles on the pleurotergites of this species.

Description of female

Total body length 333 – 415 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 166 μm.

Rostrum (Fig. 7B) triangular with tapering margins towards the front; tip bifid; dorsal surface pitted.

Habitus (Fig. 7A). Largest width near posterior margin of cephalothorax. Cephalothorax tapering strongly in anterior direction; showing a distinct constriction in the middle of the lateral margin. Pleurotergites extended laterally, except for the anal somite. First urosomite, genital double-somite and following urosomites somewhat protruded in posterior direction. Anterior part of genital double-somite less wide than posterior part.

Ventral surface of genital double-somite striated. Ventral surface of following urosomites smooth. Posteroventral margins of genital double-somite and following urosomites spinulose. Ventral surface of anal somite smooth medially, hairy laterally.

Rostrum, cephalothorax, anal somite and dorsal surface of caudal rami pitted. Pleurotergites of prosomites and urosomites with a pattern of small denticles and transversal rows of small denticles; lateral wings with more or less pits. Posterior margin of cephalothorax smooth medially, serrate laterally. Prosomites and urosomites with a distinctly serrate posterodorsal margin. Anal operculum not distinctly protruding and convex with an almost smooth margin.

Caudal rami (Fig. 7F) cylindrical and 1.7 times as long as wide. Seta I, II, III and VII implanted sub-apically. Inner margin of caudal rami undulating; outer margin straight. Inner margin furnished with two rows of long spinules.

Antennule (Fig. 7B) six-segmented; segment 1 to 4 with a pitted dorsal integument; segment 1 to 3 with spinules along the inner margin; segment 3 to 5 with spinules along the outer margin. Segment 1 proximally with a dorsal and a lateral blunt thorn. Segment 2 with a large posteriorly directed hook.

Mouthparts and P1-P4 as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1.

P5 (Fig. 7C) as in *Peltidiphonte rostrata*. Exopodite oblong. Baseoendopod and exopod furnished densely with spinules on the surface and along the margins.

Description of male

Total body length 286 – 410 μm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Rostrum (Fig. 7E). Narrower than in female; with slightly concave margins.

Habitus and length as in the female except for the slightly more slender urosome. Ventral surface of urosomites as in type species with a transversal row of spinules on third urosomite, other urosomites smooth. Posteroventral margins of third to fifth urosomite spinulose. Posterolateral wing of second urosomite rounded.

Antennule (Fig. 7E) eight-segmented; sub-chirocer. Segment 1 and 2 as in female. Integument of other segments smooth. Segment 5 with a process on the dorsal surface. Segment 6 with a small bump on the dorsal surface.

Mouthparts and P1-P4 as in female.

P5 (Fig. 7D). Baseoendopod represented as a small strip, bearing one seta. Exopodite oblong, spinulose along the lateral margins.

Differential diagnosis – *Peltidiphonte cristata* shares the same leg chaetotaxy with *P. maior*, *P. ovata* and *P. paracristata*. It differs from *P. maior* in particular by the shorter caudal rami, the much smaller body size and the shape of the posterolateral angles of the cephalothorax. It differs from *P. ovata* by the tapering rostrum, the more compressed habitus, the shape of the caudal rami and the blunt outer thorn on the first segment of the antennule. The anterior part of the genital double-somite in the female of *P. cristata* is distinctly narrower than the posterior part, whereas in the female of *P. ovata* both parts are equally wide. Moreover, the anal operculum in *P. ovata* is distinctly protruding posteriorly. *P. cristata* is closely related to *P. paracristata* but clearly differs in the shape of the caudal rami and the absence of sexual dimorphism in the exopodites of P3 and P4.

Known range – *P. cristata* is known from the Comoros (type locality).

***Peltidiphonte furcata* Gheerardyn & Fiers sp. n.** (Figure 8)

Type locality – Western Pacific Ocean, Papua New Guinea, Madang Province, Hansa Bay (Duangit Reef) (4° 10' S, 144° 53' E), coral sand and coral rubble from the east side, water depth 40 to 46 m.

Material – (a) From type locality: holotype ♀ dissected on 1 slide (COP 2439); allotype ♂ dissected on 1 slide (COP 2440); paratypes are 2 ♀♀ and 2 ♂♂ (COP 2441) preserved in 70% alcohol; all collected 28 May 1979;

(b) Western Pacific Ocean, Papua New Guinea, Madang Province, Barol Beach (east of Hansa Point) (4° 11' S, 144° 54' E), coarse sand from a tidal pool. – paratypes are 1 ♀ and 1 ♂ (COP 2442) preserved in 70% alcohol; collected 23 May 1982;

Etymology – The species name refers to the long and cylindrical caudal rami of this species.

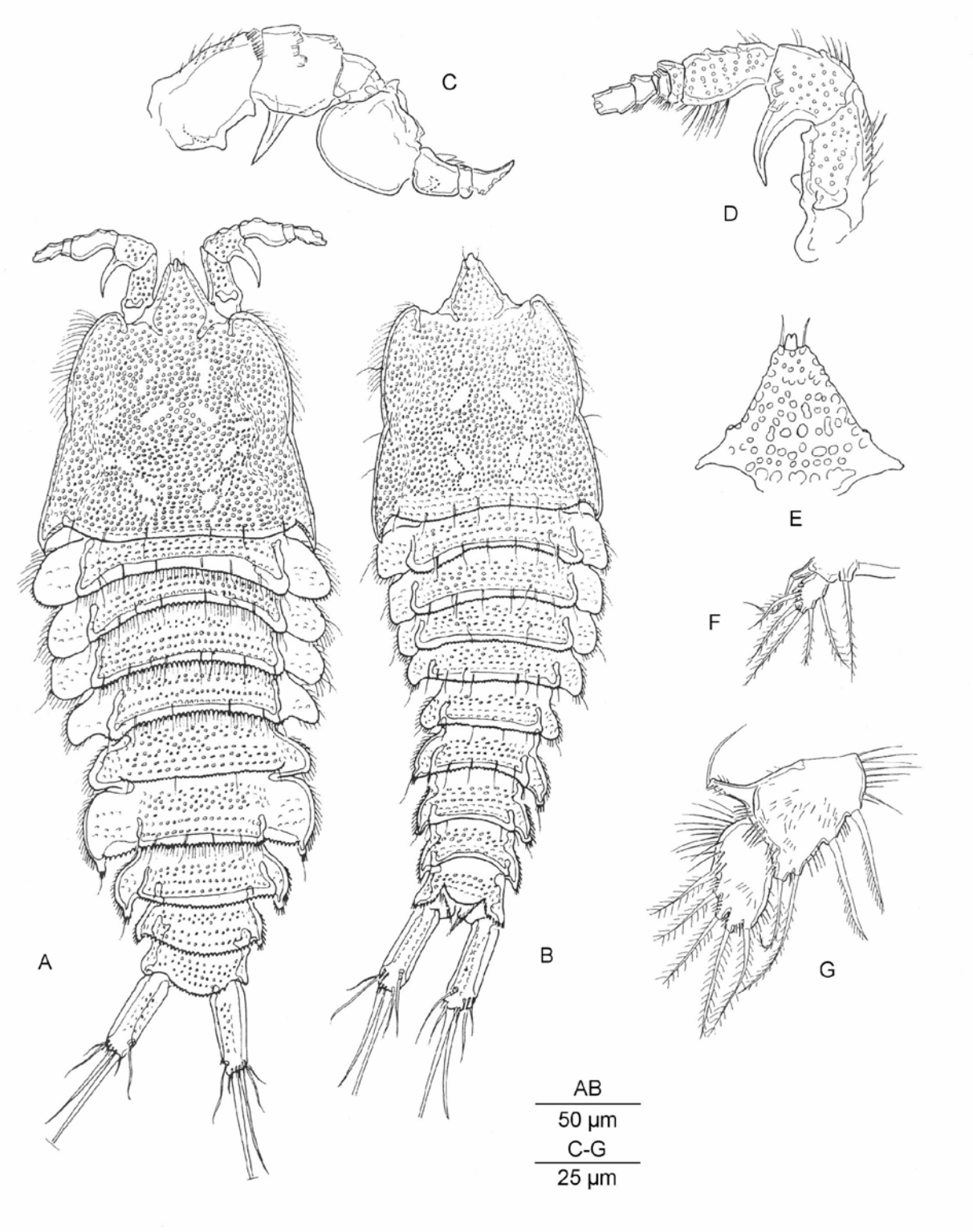

Figure 8. *Peltidiphonte furcata* sp. n. (A) female habitus, dorsal; (B) male habitus, dorsal; (C) male antennule (armature omitted), ventral; (D) female antennule (armature omitted), dorsal; (E) female rostrum, dorsal ; (F) male P5, anterior; (G) female P5, anterior.

Description of female

Total body length 350 - 420 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 135 μm.

Rostrum (Fig. 8E) large with straight lateral margins; triangular; tip small, prominent and bilobed; dorsal surface pitted.

Habitus (Fig. 8A). Body depressed; with a rather slender body-shape (comparing to its congeners). Cephalothorax slightly constricted near the middle; posterolateral angles extended into sharp points. Free prosomites and first urosomite with laterally directed rounded pleurites. Anterior part of genital double-somite only slightly extended. Following urosomites protruded in posterior direction. Anal somite with a convex anal operculum with an only slightly serrate margin. Caudal rami pitted dorsally.

Cephalothorax and pleurotergites pitted in a less dense pattern. Pleural integument of the somites with some incomplete pits. Posterodorsal margin of cephalothorax smooth; of the following somites serrate. Ventral surface of genital double-somite and anterior part of the following urosomite with fine cuticular striae. Ventral surface of the following urosomites smooth. Posteroventral margins of genital double-somite and following urosomites set with long spinules.

Caudal rami laterally furnished with minute denticles and ventrally smooth; cylindrical with straight margins and 3 times as long as wide. Setae I, II and III implanted near the distal margin; seta VI short and smooth; seta VII implanted in the distal sixth.

Antennule (Fig. 8D) seven-segmented. Integument of segment 1 to 4 pitted dorsally, of the other segments smooth. Segment 1 proximally with a dorsal and a small lateral blunt thorn; spinulose along the inner margin. Segment 2 with a large posteriorly directed hook and long spinules along inner margin. Segment 3 to 6 with long and slender spinules along the outer margin.

Mouthparts and P1-P4 as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1.

P5 (Fig. 8G). Baseoendopodite with very long spinules along the proximal inner margin and along the articulation with the exopodite; proximal spines strong and armed along one side; apical and sub-apical setae long and plumose. Exopodite ovate with long spinules along the outer margin and with 5 plumose setae.

Description of male

Total body length 330 – 390 μm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Habitus (Fig. 8B) as in female but with a more slender urosome. Ventral surface of the third urosomite with a transversal row of spinules. Posteroventral margins of third to fifth urosomite bearing a row of spinules, which are slender in the median part of the posteroventral margin of the third and fourth urosomite.

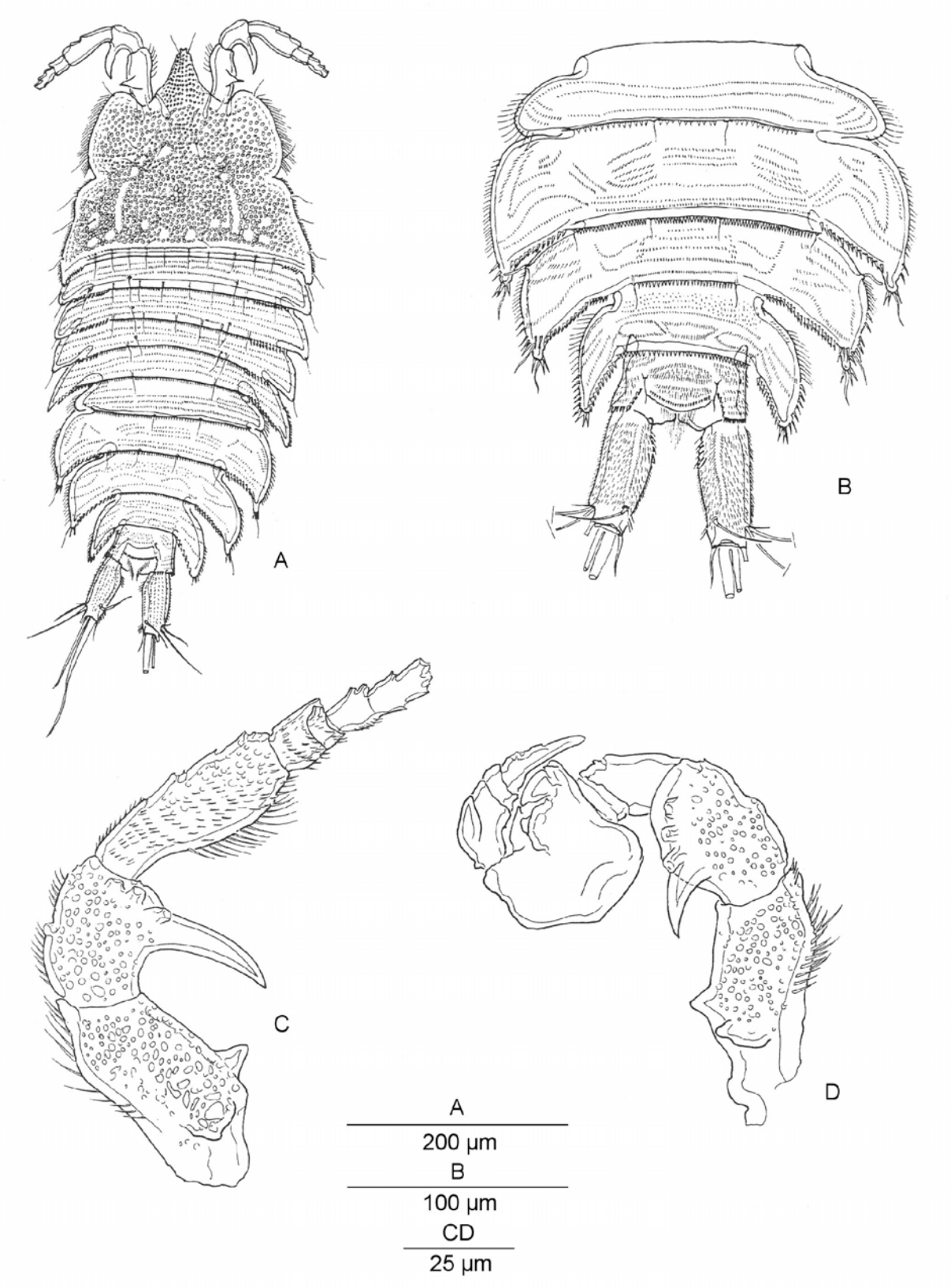

Figure 9. *Peltidiphonte maior* sp. n. (A) female habitus, dorsal; (B) female urosome, dorsal; (C) female antennule (armature omitted), dorsal ; (D) male antennule (armature omitted), dorsal.

Antennule (Fig. 8C) eight-segmented; sub-chirocer. Segment 1 and 2 as in female. Segment 3 to 8 devoid of integumental structures. Segment 6 with a blunt process dorsally along the outer margin.

Mouthparts and P1-P4 as in female.

P5 (Fig. 8F). Baseoendopodite represented as a small strip, bearing one seta. Exopodite oblong bearing five plumose setae.

P6 vestiges asymmetrical. One vestige functional; one vestige fused to somite. Both rami oblong; bearing two setae, inner one plumose, outer one naked.

Variability – The specimens from Barol Beach have somewhat shorter caudal rami, namely 2.2 to 2.6 times as long as wide. The male of *Peltidiphonte furcata* shows a somewhat variable chaetotaxy on the endopods of P3-P4. Some specimens have endopods which bear only 2 setae on enp-2 instead of 3.

Differential diagnosis – *P. furcata* is easily distinguishable from its congeners by the markedly tapering urosome, the long caudal rami, the posterolateral angles of the cephalothorax which are extended into sharp points, the more or less rounded exopodite of the female P5 and the slender body shape. The male of *P. furcata* has a distinctly slender urosome. Although the male urosome of all species of the genus is somewhat narrower than that of the female, the constriction in *P. furcata* is very conspicuous and is an important discriminating feature.

Known range – *P. furcata* is known from the northern coast of Papua New Guinea (Madang Province).

***Peltidiphonte maior* Gheerardyn & Fiers sp. n.** (Figures 9-10)

Type locality – Western Pacific Ocean, Papua New Guinea, Madang Province, Laing Island (4° 11' S, 144° 52' E), northwestern reef flat, coarse coral sand in tidal pools.

Material – (a) From type locality: holotype ♀ dissected on 3 slides (COP 2403a-c); allotype ♂ dissected on 2 slides (COP 2404a-b); 1 ♀ paratype dissected on 3 slides (COP 2405a-c) and 27 paratypes (COP 1942) preserved in 70% alcohol; all collected on 8 May 1978.

(b) Western Pacific Ocean, Papua New Guinea, different locations in Madang Province [Laing Island (4° 11' S, 144° 52' E), Legoarant Island (4° 18' S, 145° 1' E), Kabak Plantation (east of Kumbug Bay) (4° 23' S, 145° 9' E), Barol Beach (east of Hansa Point) (4° 11' S, 144° 54' E), Podbielsky Point (4° 15' S, 144° 58' E), Talia Point (4° 18' S, 144° 59' E)], coral sand, tidal and subtidal zone to a water depth of 12 m. – paratypes are 4 ♀♀ and 5 ♂♂ dissected on slides (COP 4658 – COP 4666) and numerous ♀♀ and ♂♂ (COP 2411 – COP 2423, COP 2425 – COP 2428) preserved in 70% alcohol; collected in May 1977, May 1978, June 1979, July 1981, May 1982 and June 1982.

Etymology – The species name refers to the large size of this species in comparison with the other members of the genus.

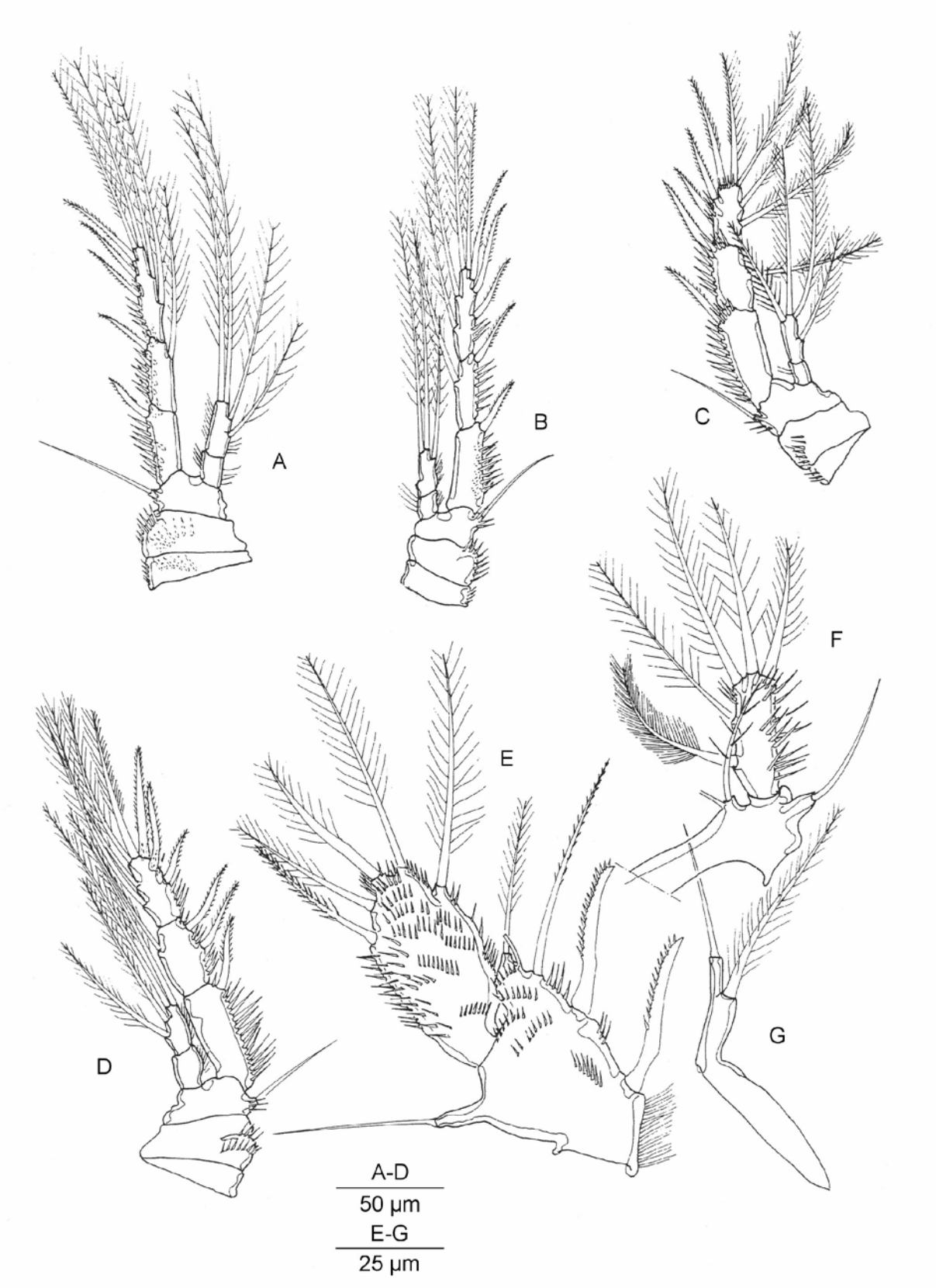

Figure 10. *Peltidiphonte maior* sp. n. (A) female P3, posterior; (B) female P4, posterior; (C) male P4, anterior; (D) male P3, anterior; (E) female P5, anterior; (F) male P5, anterior; (G) male P6, anterior.

Description of female

Total body length 505-600 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 238 μm.

Rostrum large; prominent and tapering towards the tip; lateral margins concave; dorsal surface pitted; tip bifid.

Habitus (Fig. 9A, 9B). Body depressed. Largest width near posterior margin of cephalothorax. Cephalothorax flattened with curved margins and constricted in the middle. Posterolateral angles of cephalothorax extended into sharp points. Pleurotergites of free prosomites widening posteriorly, somewhat extended in posterior direction. Anterior part of genital double-somite rather small, fitting into the protruded wings of the first urosomite. Following urosomites (except anal somite) broad and winged, posteriorly extended.

Cephalothorax pitted; having a symmetrical pattern of smooth areas; posterior margin smooth but strongly serrate near the posterolateral extensions. Pleurotergites of the somites with a pattern of transversally arranged denticles. Posterodorsal margins of the somites serrate. Caudal rami densely covered with small spinules except for a small smooth strip on the dorsal surface; dorsal surface with some pits.

Ventral surface of genital double-somite striated, of the following urosomites smooth. Ventral surface of anal somite hairy laterally and smooth in the middle. Posteroventral margin of genital double-somite smooth in the middle and hairy along some distance of the lateral side; idem for the following somite but set with small spinules in the middle. Posteroventral margins of the penultimate urosomite and the anal somite with strong spinules.

Caudal rami 2.5 times as long as wide; cylindrical; having a slightly convex inner margin and a straight outer one. Seta VII implanted in the distal fourth; other setae similar to the type species.

Antennule (Fig. 9C) six-segmented (Segment 6 can have an indistinct transverse suture). Segment 1 with a dorsal and a lateral blunt thorn. Segment 2 with a large posteriorly directed hook. Dorsal surface of segment 1 and 2 strongly pitted and set with long spinules along the inner margin. Segment 3 to 5 with spinules on the dorsal surface and along the outer margin.

Mouthparts and P1-P4 as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1. Anterior surfaces of the rami are clothed with somewhat longer spinules comparing to the type species (Fig. 10A, 10B).

P5 (Fig. 10E). Proximal baseoendopodal spines strong, armed along one side; sub-apical and apical setae plumose. Exopodite ovate bearing five plumose setae. Surface of baseoendopodite and exopodite furnished with several rows of spinules.

Description of male

Total body length 451 – 590 μm (measured from anterior margin of rostrum to posterior margin of caudal rami).

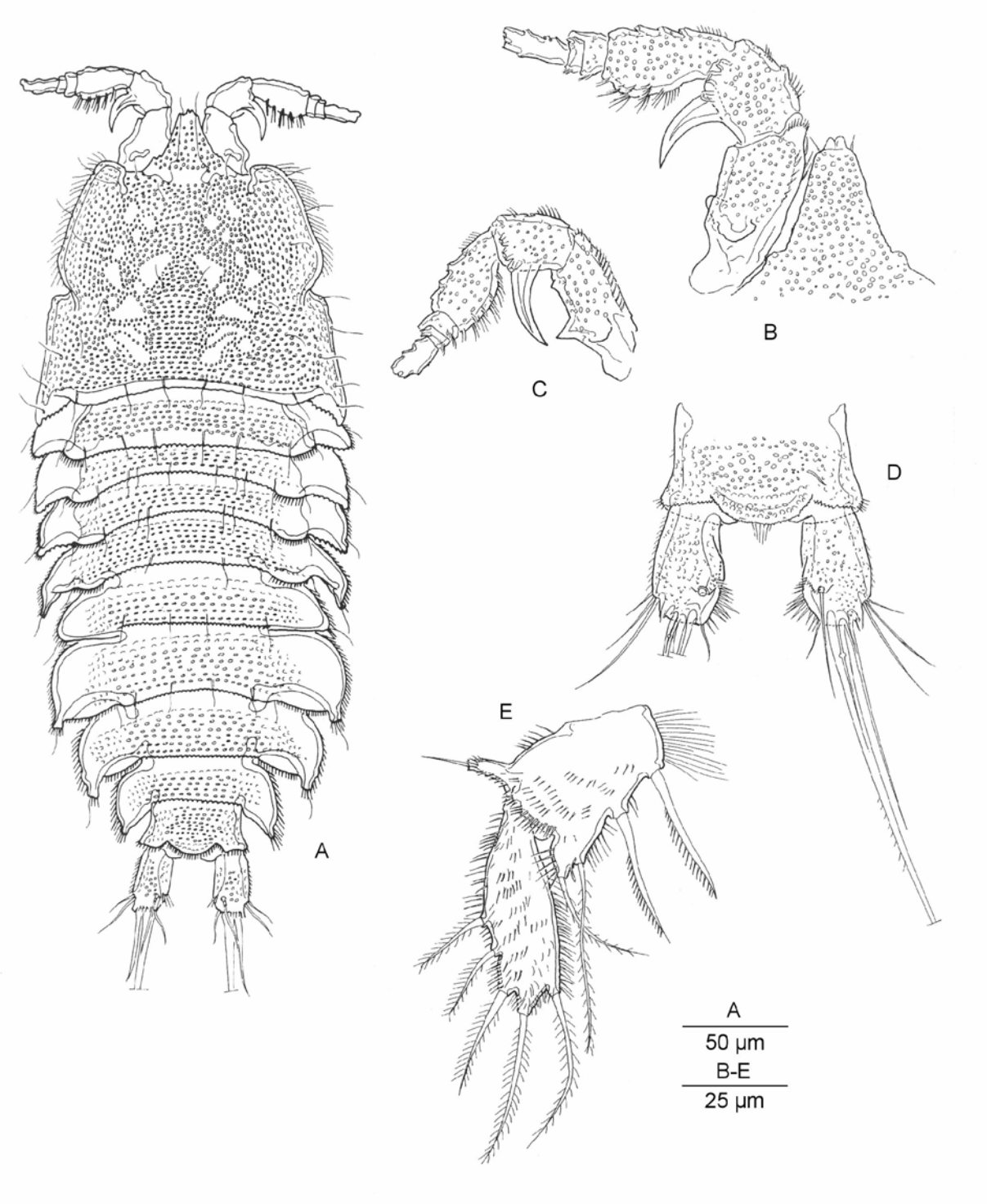

Figure 11. *Peltidiphonte morovoensis* sp. n. (A) female habitus, dorsal ; (B) female antennule (armature omitted) and rostrum, dorsal; (C) female antennule (paratype, armature omitted), dorsal; (D) female caudal rami, dorsal; (E) female P5, anterior.

Habitus as in female except for a more slender urosome. Ventral surface of the third urosomite with a transversal median row of spinules. Posteroventral margins of third to fifth urosomites bearing a row of strong spinules.

Antennule (Fig. 9D) eight-segmented; sub-chirocer. Segment 1 and 2 as in female. Segment 6 with a distinct dorsal process.

Mouthparts, P1 and P2 as in female.

Exopodal segments and outer spines of P3 and P4 more robust than in female (Fig. 10D, 10C). Outer terminal element on exp-3 rigid. Outer seta of enp-2 of P4 with slightly stronger setules.

P5 (Fig. 10F). Baseoendopod bearing one plumose seta. Exopodite oblong, having long spinules along the outer margin and bearing five plumose setae.

P6 (Fig. 10G) vestiges asymmetrical.

Variability – In the holotype the P2 has 2 inner setae on one side but only 1 inner seta on the other side. The setal formula of this segment is very variable. Specimens with 2 inner setae are as common as specimens with only 1 inner seta. The median exopodal segment of the allotype P3 bears 2 outer spines (Fig. 10D) but has normally 1 outer spine.

Differential diagnosis – *Peltidiphonte cristata*, *P. maior*, *P. ovata* and *P. paracristata* have swimming legs with the same setal formulae. However, *P. maior* differs from its congeners in several aspects: the shape of the posterolateral angles of the cephalothorax, the length/width-ratio of the caudal rami, the length of the body and the more strongly developed male exopods of P3 and P4.

Known range – *P. maior* is known from the northern coast of Papua New Guinea (Madang Province).

Peltidiphonte morovoensis **Gheerardyn & Fiers sp. n.** (Figure 11)

Type locality – Western Pacific Ocean, Solomon Islands, Uipi Island, Morovo Lagoon (8° 29' S, 158° 4' E), sediments from the reef flat.

Material – (a) From type locality: holotype ♀ dissected on 2 slides (COP 2443a-b); paratype is 1 ♀ (COP 2444) preserved in 70% alcohol; collected 2 November 1982;

(b) Western Pacific Ocean, Australia, Queensland, John Brewer Reef (18° 38' S, 147° 4' E), sediments collected near the basis of the reef, water depth 3 m. – paratypes are 1 ♂ on 1 slide (COP 4668), 1 ♀ dissected on 2 slides (COP 4667a-b) and 1 ♀ (COP 2445) preserved in 70% alcohol; collected 24 May 1984.

Etymology – The species name refers to the type locality of this species.

Description of female

Total body length 342 – 370 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 148 μm.

Rostrum (Fig. 11B) strongly prominent; rather narrow; lateral margins tapering in front; tip bifid; pitted dorsally.

Habitus (Fig. 11A) typical for the genus. Cephalothorax tapering in front and distinctly constricted in the middle. Posterolateral angles of cephalothorax slightly extended and posteriorly directed. Prosomites and urosomites laterally extended. Anterior part of genital double-somite with rounded lateral margins. Posterior part of genital double-somite and following urosomites (except anal somite) with posteriorly directed extensions. Anal operculum convex with a slightly serrate margin.

Integument of cephalothorax and pleurotergites of prosomites and urosomites entirely and densely pitted. Pleural areas of the prosomites less densely pitted. Posterodorsal margin of cephalothorax smooth but distinctly serrate near the lateral extensions. Posterodorsal margins of prosomites and urosomites serrate along the tergital and pleural margin and distinctly serrate along a small convex part near the transition of both plates.

Ventral surface of genital double-somite striated; of the following urosomites smooth. Posteroventral margins of genital double-somite and following urosomites spinulose.

Caudal rami (Fig. 11D) 1.7 times as long as wide; pitted dorsally; smooth ventrally; outer margin straight bearing small spinules; inner margin smooth except for a short transversal row of spinules near the implantation of seta VII; inner margin distally slightly convex, forming dorsally a bump upon which stands seta VII. Seta I, II, III and VII implanted sub-apically.

Antennule (Fig. 11B) six-segmented. Segment 1 to 4 pitted dorsally. Spinules on the inner margin of segment 1 to 3 and along the outer margin of segment 3 to 5. Integument of segment 5 and 6 smooth. Segment 1 proximally with a dorsal and a small lateral blunt thorn. Segment 2 with a long posteriorly directed hook.

Mouthparts and P1-P4 as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1.

P5 (Fig. 11E). Baseoendopodite with long spinules along the proximal inner margin and along the articulation with the exopodite. Baseoendopodite and exopodite covered with spinules. Exopodite elongate.

Description of male

Total body length 350 μm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Habitus as in female; but distinctly slender. Especially the urosome is remarkably slender. Ventral surface of the third urosomite with a tranversal row of spinules. Posteroventral margins of third to fifth urosomite bearing a row of spinules; which are small and slender medially and conspicuous long and strong more laterally.

Antennule eight segmented; sub-chirocer. Segment 1 and 2 as in female.

Mouthparts and P1-P4 as in female.

P5. Baseoendopodite represented as a small strip, bearing one seta. Exopodite oblong bearing five plumose setae.

Variability – The thorn on the outer margin of the first segment of the A1 seems to be variable, namely blunt (Fig. 11B) or sharp (Fig. 11C).

Differential diagnosis – *Peltidiphonte morovoensis* is one of the species with a reduced chaetotaxy of the endopodites. The male of *P. morovoensis* has a distinctly slender urosome as is the case in *P. furcata*. Males of both species however are clearly discriminated by the shape and length of the caudal rami. The posterolateral angles of the cephalothorax are distinctly sharp in *P. furcata* and rather rounded in *P. morovoensis*.

Known range – *P. morovoensis* is known from the Solomon Islands (type locality) and from the Great Barrier Reef.

***Peltidiphonte ovata* Gheerardyn & Fiers sp. n.** (Figures 12-13)

Type locality – Egypt, Red Sea, Strait of Tiran, Gordon Reef (27° 59' N, 34° 27' E), sand sample, water depth 2 to 3 m.

Material – (a) From type locality: holotype ♀ dissected on 1 slide (COP 2447); allotype ♂ dissected on 1 slide (COP 2448); paratypes are 2 ♂♂ (COP 2449) and 1 ♂ (COP 4669) preserved in 70% alcohol; all collected 11 November 1983;

(b) Egypt, Red Sea, Orifa, Ras Umm Sid (27° 51' N, 34° 17' E), sand sample, water depth 10 m. – paratype is 1 ♂ (COP 2446) preserved in 70% alcohol; collected 11 April 1986;

(c) Western Indian Ocean, different locations along Kenyan coast [Msambweni (4° 28' S, 39° 29' E), Diani Beach (4° 18' S, 39° 35' E), Watamu Marine Park (3° 21' S, 40° 1' E)], dead coral fragments and coral sand, water depth from 3 m to less than 0.5 m. – paratypes are 3 ♀♀ and 2 ♂♂ dissected on slides (COP 4671 – COP 4675) and 38 ♀♀ and 16 ♂♂ (COP 4670), 20 ♀♀ and 20 ♂♂ (COP 4676), 1 ♂ (COP 4677), and 1 ♀ (COP 4678) preserved in 70% alcohol; collected in February 2002.

Etymology – The species name refers to the body shape of this animal.

Description of female

Total body length 381 – 480 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 200 μm.

Rostrum (Fig. 12G) broad; widening posteriorly; bifid tip with broad lips; rostral tip strongly prominent; dorsally pitted; robust appearance.

Habitus (Fig. 12A). Body ovate in dorsal view. Each somite (except anal somite) laterally extended. Cephalothorax with a distinct constriction near the middle. Anterior part of genital double somite as broad as posterior part.

Cephalothorax and dorsal surface of the caudal rami pitted. Lateral sides of cephalothorax with small denticles. Pleurotergites of prosomites and urosomites with a pattern of small denticles and rows of small denticles. Posterior margin of cephalothorax smooth medially and distinctly serrate laterally. Posterior margins of the somites serrate. Posterior margins of the urosomites

with larger incisions laterally than medially. Anal operculum distinctly protruding and convex; with a serrate margin and with some pits on the dorsal surface.

Ventral surface of genital double somite striated; of the following urosomites smooth. Posteroventral margins of the genital double-somite and of the following urosomites spinulose.

Caudal rami (Fig. 12C) 2 times as long as wide with straight outer and convex inner margin. Setae I, II, III and VII implanted sub-apically. Caudal rami pitted dorsally, hairy ventrally. Outer margin of the rami furnished with slender spinules; inner margin with a row of strong spinules.

Antennule (Fig. 12B) six-segmented. Segment 1 and 2 with a pitted dorsal integument. Segment 3 and 4 with rows of small denticles. Segment 5 and 6 smooth. Segment 1 with a blunt thorn dorsally on the proximal half and a large, sharp thorn along the outer margin. Segment 2 with a large posteriorly directed hook.

Mouthparts and P1-P4 as in *Peltidiphonte rostrata*. Swimming leg setal formula in table 1.

P5 (Fig. 13A) as in *Peltidiphonte rostrata*. Proximal outer seta of the exopodite implanted on a distinct bump.

Description of male

Total body length 326 – 470 μm (measured from anterior margin of rostrum to posterior margin of caudal rami).

Rostrum (Fig. 12F) less wide as in female.

Habitus as in female, except for a more slender urosome. Transversal row of spinules on ventral surface of the third urosomite. Lateral wing of the second urosomite rounded. Posteroventral margins of third to fifth urosomite with strong spinules.

Antennule (Fig. 12E) eight-segmented; sub-chirocer. Integument of segment 1 and 2 as in female, the other segments smooth. Sharp thorn on outer margin of segment 1 smaller as in female. Segment 6 with a strong blunt process on the outer margin.

Mouthparts and P1-P4 as in female.

P5 (Fig. 12D). Baseoendopodite bearing 1 seta with a tube pore and a bump medially from it. Exopodite oblong with five slender, plumose setae.

Variability – The specimens from the Kenyan coast have shorter caudal rami (1.6 times as long as wide) and a male antennule which has a slightly smaller outer thorn on the first segment and lacks a process on the sixth segment (Fig. 12F).

Differential diagnosis – *Peltidiphonte cristata*, *P. maior*, *P. ovata* and *P. paracristata* have swimming legs with the same setal formulae. However, *P. ovata* differs from its congeners by the ovate habitus, the robust rostrum, the conspicuous broad anterior part of the genital double-somite, the shape of the caudal rami and the protruding anal operculum.

Known range – *P. ovata* is known from the Red Sea (type region) and the Kenyan coast.

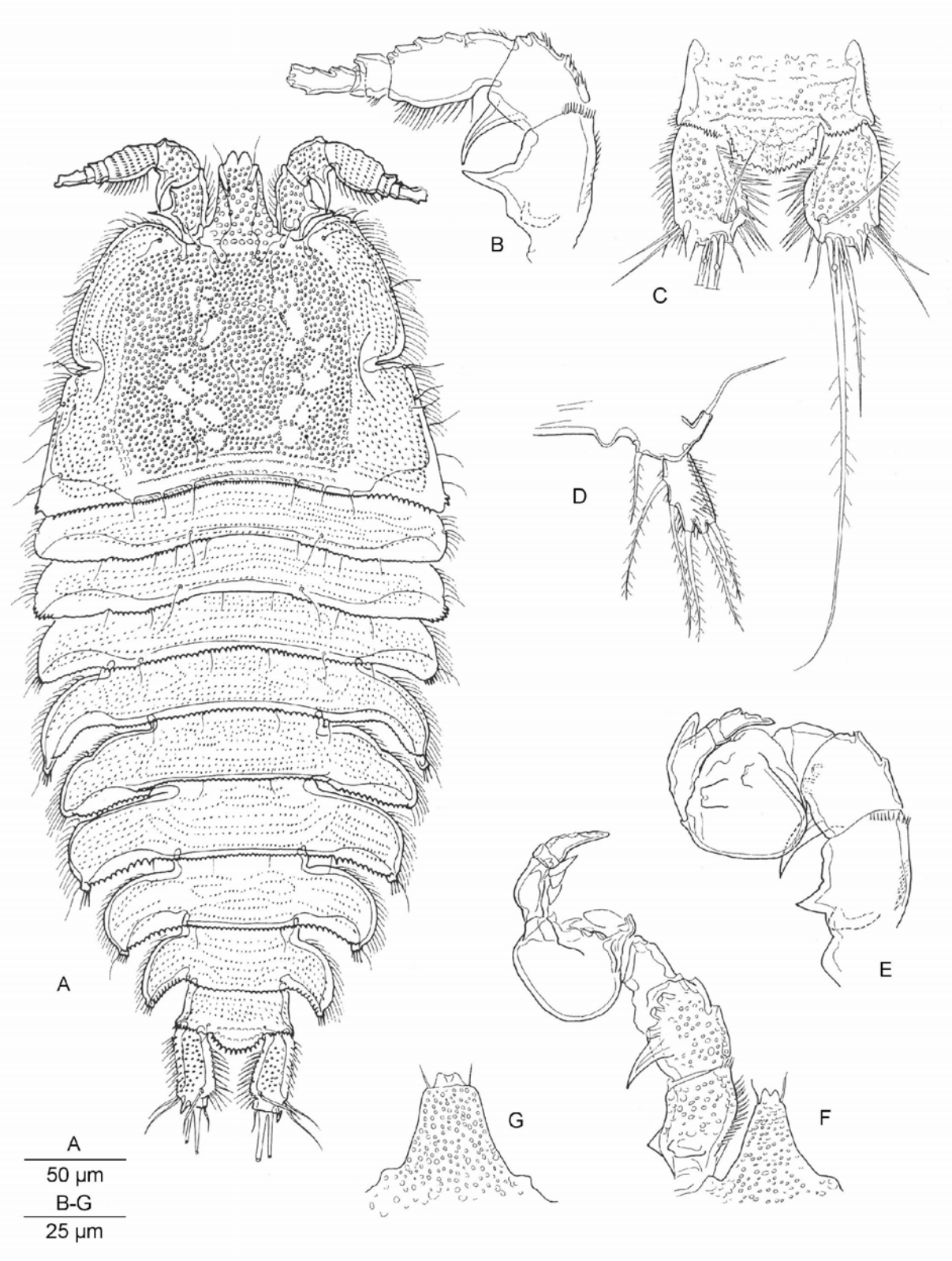

Figure 12. *Peltidiphonte ovata* sp. n. (A) female habitus, dorsal; (B) female antennule (armature omitted), ventral; (C) female caudal rami, dorsal; (D) male P5, anterior; (E) male antennule (armature omitted), ventral; (F) male antennule and rostrum (paratype, armature omitted), dorsal; (G) female rostrum, dorsal.

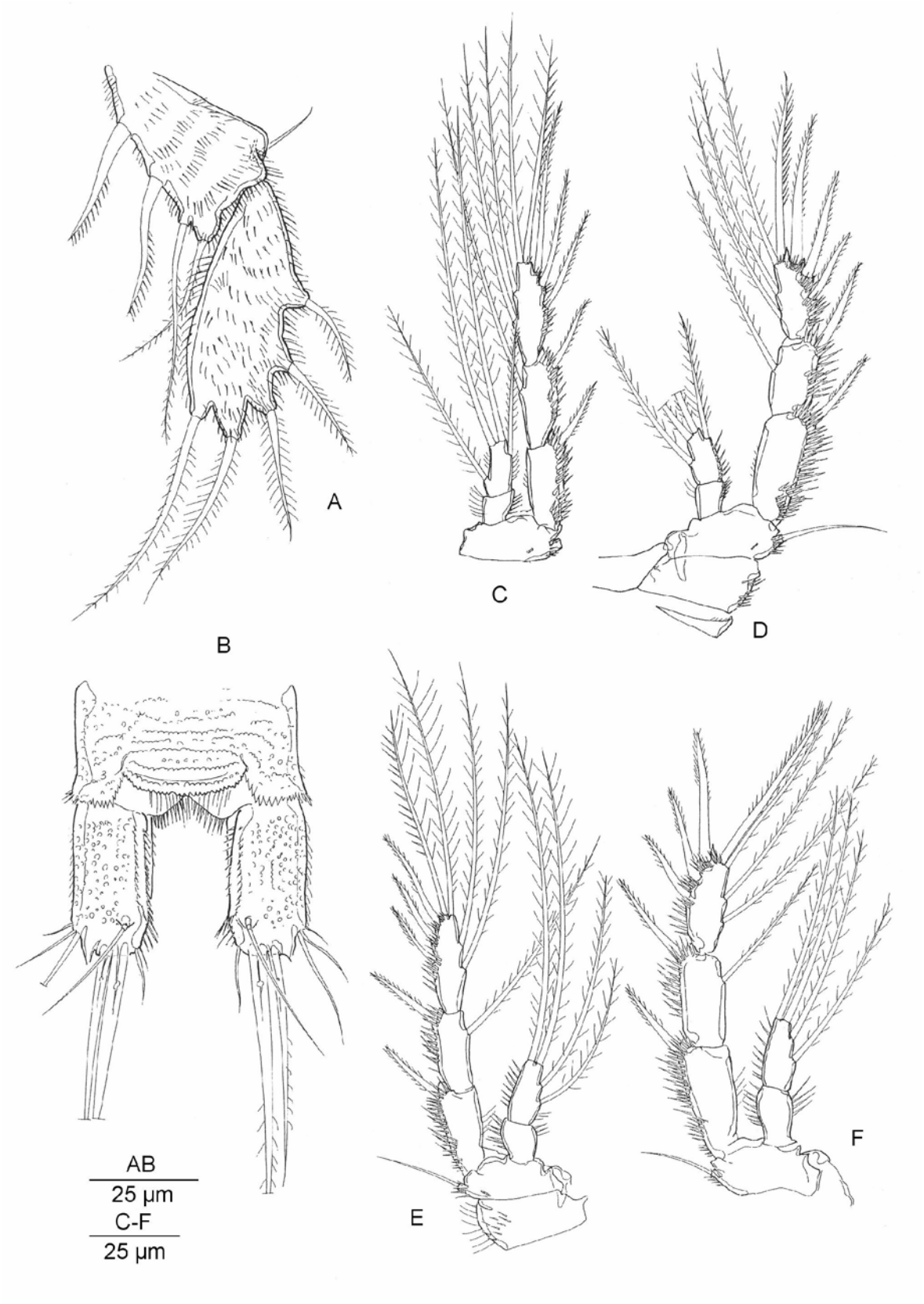

Figure 13. *Peltidiphonte ovata* sp. n. (A) female P5, anterior; *Peltidiphonte paracristata* sp. n. (B) female caudal rami, dorsal; (C) female P4, anterior; (D) male P4, anterior; (E) female P3, anterior; (F) male P3, anterior.

***Peltidiphonte paracristata* Gheerardyn & Fiers sp. n.** (Figure 13)

Type locality – Western Indian Ocean, Kenyan coast, Tiwi Beach (4° 14' S, 39° 36' E), dead coral fragments, water depth less than 1 m.

Material – (a) From type locality: holotype ♀ on 1 slide (COP 4679); allotype ♂ on 1 slide (COP 4680); paratypes are 1 ♀ and 1 ♂ dissected on slides (COP 4681 – COP 4682); all collected 22 February 2002;

(b) Western Indian Ocean, different locations along the Kenyan coast [Diani Beach (4° 18' S, 39° 35' E), Msambweni (4° 28' S, 39° 29' E)], dead coral fragments, water depth 3 m to less than 0.5 m. – paratypes are 1 ♀ dissected on 2 slides (COP 4685) and 2 ♂♂ (COP 4683), and 1 ♀ and 8 ♂♂ (COP 4684) preserved in 70% alcohol; all collected in February 2002;

(c) Western Indian Ocean, Comoros, different locations on Grande Comore [Moroni (11° 42' S, 43° 14' E), Foumbouni (11° 51' S, 43° 29' E)], sand samples, different water depths (11 m to 84 m). – paratypes are 2 ♂♂ and 1 ♀ dissected on slides (COP2430, COP 4687 – COP 4688) and 4 ♀♀ and 4 ♂♂ (COP 4686), 2 ♀♀, 2 ♂♂ and 1 CIV (COP 4689), 3 ♀♀ and 2 ♂♂ (COP 2434) and 4 ♀♀, 4 ♂♂ and 1 ♂CV (COP 2435) preserved in 70% alcohol; all collected in August 1981.

Etymology – The species name refers to the close relationship with *Peltidiphonte cristata*.

Female

Total body length 394 - 531 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 179 μm.

Caudal rami (Fig. 13B) cylindrical and 2 times as long as wide. Seta I, II, III and VII implanted sub-apically. Inner and outer margin of caudal rami straight; inner margin furnished with two parallel continuous rows of spinules along the entire length.

All other diagnostic features correspond to those encountered in *Peltidiphonte cristata* sp. n.

Male

Total body length 366 – 518 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 160 μm.

Caudal rami as in female.

Exopodal segments and outer spines of P3 and P4 more robust than in female (Fig. 13C, 13D, 13E, 13F). Outer terminal element on exp-3 rigid, with a more dense and spinule-like ornamentation along outer side of stem. Outer seta of enp-2 of P4 with slightly stronger setules.

All other diagnostic features correspond to those encountered in *Peltidiphonte cristata* sp. n.

Differential diagnosis – *Peltidiphonte paracristata* is closely related to *P. cristata* but clearly differs in the shape of the caudal rami. Moreover the exopodites of P3 and P4 show sexual dimorphism which is an important characteristic.

Known range – *P. paracristata* is known from the Kenyan coast and the Comoros.

Key to the species of *Peltidiphonte* gen. n.

1. Rostrum with parallel margins and truncated at the tip.....*Peltidiphonte rostrata* sp. n.
   Rostrum tapering towards the tip, more or less triangular.....2
2. Setal formula of enp-2 P2-P4: 220 or 120, 220 and 121.....3
   Setal formula of enp-2 P2-P4 different.....6
3. Caudal rami 2.5 times as long as wide. Posterolateral angles of the cephalothorax extended into sharp points. Large (total body length: ♀: 505-600 μm, ♂: 451-590 μm) animals.....
   .....*Peltidiphonte maior* sp. n.
   Caudal rami 2 times as long as wide at the most. Posterolateral angles of the cephalothorax not extended. Smaller (total body length: ♀: 333-531 μm, ♂: 286-518 μm) animals.....4
4. Process along the outer margin of segment 1 of A1 large (length is approx. 2/3 of the width of segment 1) and sharp in female, smaller and sharp in male. Anterior and posterior part of the genital double-somite of the female equally wide. Distinctly protruding anal operculum. Inner margin of the caudal rami distinctly convex.....*Peltidiphonte ovata* sp. n.
   Process along the outer margin of segment 1 of A1 rather small (length is approx. 1/3 of the width of segment 1) and blunt. Anterior part of the genital double-somite of the female less wide than posterior part. Anal operculum not protruding. Inner margin of the caudal rami straight or slightly undulating.....5
5. Inner margin of caudal rami undulating. No sexual dimorphism in exopods of P3-P4.....
   .....*Peltidiphonte cristata* sp. n.
   Inner margin of caudal rami straight. Sexual dimorphism in exopods of P3-P4.....
   .....*Peltidiphonte paracristata* sp. n.
6. Setal formula of enp-2 P2-P4: 120, 110, 110. Endopods of P2-P4 very compact, not reaching beyond the corresponding exp-1. Compact caudal rami (length-width ratio: 1.3).....
   .....*Peltidiphonte andamanica* sp. n.
   Setal formula of enp-2 P2-P4: 120, 120, 120. Endopod of P2 reaching beyond middle of exp-2; endopod of P3 only slightly longer than exp-1; endopod of P4 as long as exp-1. Caudal rami not compact (length-width ratio > 1.3).....7
7. Caudal rami 3 times as long as wide. Posterolateral angles of the cephalothorax extended into sharp points. Female A1 7-segmented. Exopod of female P5 rounded.....*Peltidiphonte furcata* sp. n.
   Caudal rami 1.7 times as long as wide. Posterolateral angles of the cephalothorax only slightly extended and posteriorly directed. Female A1 6-segmented. Exopod of female P5 ovate.....*Peltidiphonte morovoensis* sp. n.

4.5. DISCUSSION

Peltidiphonte gen. n. is placed in the family Laophontidae and more specifically in the subfamily Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000 based on the following synapomorphies as defined by Huys & Lee (2000): male antennule with up to 3 segments distal to geniculation, mandible uniramous, maxilliped with maximum 2 setae on syncoxa, P1 enp-1 without inner seta, P2 enp-2 without outer spine, proximal outer setae of female P5 exopod with distinctly separated insertion sites and absence of cup-shaped transformed pores on legs or somites.

Peltidiphonte gen. n. is clearly defined by the following combination of apomorphies: the extremely depressed body; the shape of the antennule, bearing two processes on the first segment (one on the dorsal surface and one along the outer margin) and a hook-like process along the outer margin of the second segment; the absence of sexual dimorphism in the endopodites and the absence of an outer seta on enp-2 of P3. Distinction between the species of the new genus is based upon the chaetotaxy of the endopodites, the shape of the rostrum, the number of segments of the antennule, the shape and dimensions of the processes on the first and second segment of the antennule, the shape of P5, the shape of the caudal rami, and the integumental structures on the dorsal surface.

At present, the overall phylogeny of the Laophontidae is poorly understood. Lang's (1948) phylogenetic scheme of the Laophontidae included only 19 genera, six of which being placed in other, existing or new, families since (Huys & Lee, 2000 and references herein). Moreover, the family has been expanding since, at present containing 63 genera (including that described in this paper) (Huys & Lee, 2000). The same authors divided the family in two subfamilies and made a thorough phylogenetic analysis of the newly established subfamily of Esolinae Huys & Lee, 2000. The other subfamily Laophontinae, containing 95% of the species, also needs a phylogenetic analysis to clarify the relationships between the genera. The present new genus indicates the true diversity of the family is still far from known and its specific habitus illustrates the wide variety of body forms within the family.

The depressed body shape is characteristic for the families Peltidiidae and Porcellidiidae and is also found in certain genera and species of Hamondiidae, Harpacticidae and Thalestridae. Within the Laophontidae, some genera and species (e.g. *Asellopsis* Brady & Robertson, 1873, *Platylaophonte* Bodin, 1968, *Applanola hirsuta* (Thompson & A. Scott, 1903)) approach this body shape, but their bodies are not as depressed as in the newly established genus, to which they are not directly related. The depressed and very broadened body shape in *Peltidiphonte* gen. n. is an important characteristic, which is consistent throughout the genus. *Peltidiphonte furcata* sp. n. and the male of *Peltidiphonte morovoensis* sp. n. are not as broad, but show the laterally extended and backwardly produced prosomites and urosomites.

In some harpacticoid genera (e.g. *Scutellidium* Claus, 1866, *Porcellidium* Claus, 1860) the dorsoventral flattening of the body is an adaptation to live on the smooth, flat surfaces of macroalgae, decreasing the risk of being swept away by strong water currents impacting on such surfaces (Noodt, 1971; Hicks, 1980). Similarly, the dorsoventral flattening of *Peltidiphonte* gen. n. is

assumed to be an adaptation to life on coral fragments in an environment with strong currents. While in *Porcellidium* mouthparts and first pereiopod form a ventral sucker that allows attachment to the substrate (Tiemann, 1986), in the new genus the typical P1 and Mxp of the Laophontidae serve as effective grappling hooks to embrace fine microhabitat structures (Hicks, 1980) that can be found in the complex microtopography of dead coral fragments.

Indeed, specimens of *Peltidiphonte* gen. n. were collected from the washings of large coral fragments and coarse coral gravel. This suggests a close affinity of the new genus with this substrate. However, they were also found in sediment samples. The dorsoventral flattening of *Peltidiphonte* gen. n. represents an adaptation to an epifaunal lifestyle on the surface of dead coral substrates, but the genus apparently retains the ability to live in the sediment.

The characteristic processes on the first and second segment of the antennule also occur in other genera of the Laophontidae, such as in *Amerolaophontina* Fiers, 1991, *Galapalaophonte* Mielke, 1981, *Indolaophonte* Cottarelli, Saporito & Puccetti, 1986, *Langia* Wells & Rao, 1987, *Laophontina* Norman & T. Scott, 1905 and *Wellsiphontina* Fiers, 1991b. These genera have adapted to an endobenthic and interstitial life through their cylindrical body shape and the reduced endopodites and exopodites of the swimming legs. Presumably, the strong structures on the proximal segments of the antennule serve in the locomotion between sand grains. *Peltidiphonte* gen. n. represents a lineage which retained the characteristic processes on the antennule but became dorsoventrally flattened to live as epifauna.

Apart from the striking resemblance of the antennular morphology in these genera, the ornamentation of the exopodal setae of the antenna appears to be identical. In all laophontid genera having a well developed antennal exopodite the one-segmented ramus bears 4 elements which are either plumose or pinnate. Common to *Peltidiphonte* gen. n. and the above mentioned genera is that one of the lateral elements (the one inserted on the margin directed towards the abexopodal side) is bare while the 3 other elements have a pinnate appearance. In *Peltidiphonte* gen. n. the naked seta is rather short (shorter than the other elements) and slender. In contrast, in the genera *Laophontina* and *Galapalaophonte* this element is much longer, while it is completely absent in the genera *Langia* and *Indolaophonte*.

In the new genus the exopodites of the swimming legs show the complete, conservative setation on the second and third segments, while the endopodites have a rather advanced setation. The outer spine on enp-2 of P2 is absent as is the case in all laophontinids. Moreover, in the new genus the outer spine on enp-2 of P3 is also absent. The absence of a sexually dimorph apophysis on the male P3 endopod results from the loss of its homologue (the outer spine on enp-2) in the female. Within the laophontinid genera, which have non-reduced swimming legs with 2-segmented endopods and 3-segmented exopods, the reduction of the outer spine on enp-2 of P3 occurs only in *Echinolaophonte* Nicholls, 1941 and certain species of *Paralaophonte* Lang, 1944, *Tapholeon* Wells, 1967 and *Laophonte* Philippi, 1840 (e.g. *Paralaophonte aenigmaticum* Wells, Hicks & Coull, 1982, *Tapholeon ornatus* Wells, 1967, *Laophonte ifalukensis* Vervoort, 1964). Certain species of *Peltidiphonte* gen. n. further have lost the outer spine on enp-2 of P4.

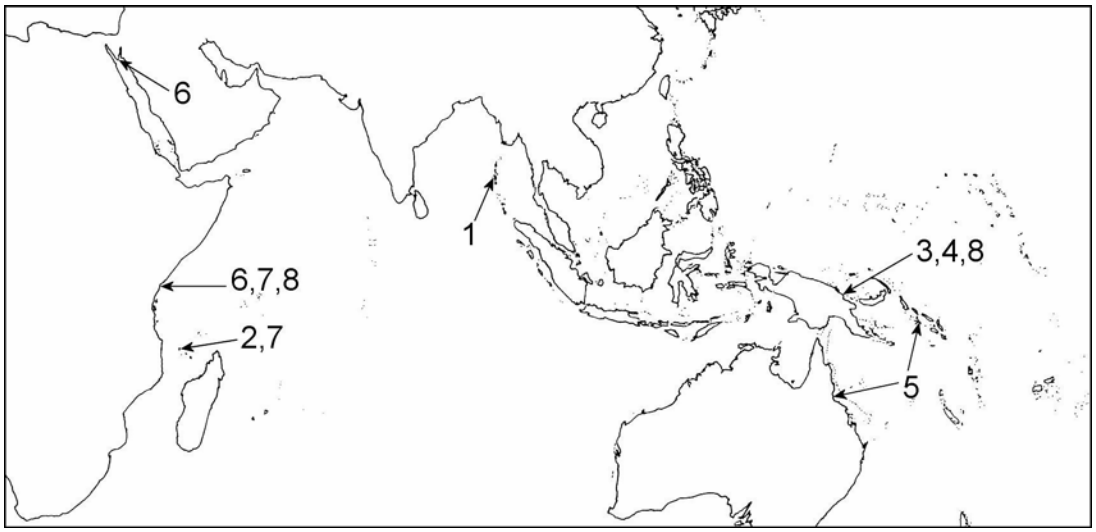

Figure 14. Map of the Indo-West Pacific Ocean showing the sampling locations of the eight presently known *Peltidiphonte* gen. n. species. (1) *Peltidiphonte andamanica* sp. n., Andaman Islands; (2) *P. cristata* sp. n., Comoros; (3) *P. furcata* sp. n., northern coast of Papua New Guinea; (4) *P. maior* sp. n., northern coast of Papua New Guinea; (5) *P. morovoensis* sp. n., Solomon Islands and northeastern coast of Australia; (6) *P. ovata* sp. n., Kenyan coast and Red Sea; (7) *P. paracristata* sp. n., Kenyan coast and Comoros; (8) *P. rostrata* sp. n., Kenyan coast and northern coast of Papua New Guinea.

Distribution

Peltidiphonte gen. n. has a distribution covering the Indo-West Pacific (Fig. 14). In the course of an extensive study of the family Laophontidae (Fiers, 1988), samples from different substrates, including washings of algae, interstitial samples in mangroves, sediments, coarse coral sand and gravel, collected in the Caribbean region were also studied. These samples did not reveal any representatives of *Peltidiphonte* gen. n., implying the absence of this genus in the Caribbean region or the need for more samples of coral fragments.

4.6. ACKNOWLEDGEMENTS

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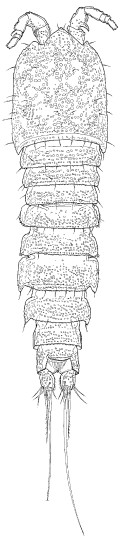
The materials on which this paper is based have been collected in the following regions and by the following persons or groups:

Andaman Islands: 1983, W. Wellens & H. De Brauwer; Comores Islands: 1981, Groupe Plongée de l'Expedition Karthala, 1985, W. Wellens; Kenya : 2002, M. Raes; Papua New Guinea: 1977, 1978, 1981, J. Van Goethem, 1979, J. Pierret, D. Christensen, 1982, K. Wouters; Red Sea: 1983, A. Brauwer & H. Smedt, 1986, W. Wellens; Solomon Islands: 1982, A. Coomans.

CHAPTER 5

Two new genera of Laophontidae (Copepoda: Harpacticoida) without sexual dimorphism in the endopods of the swimming legs



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Zootaxa 1327: 41-62.

5.1. ABSTRACT

Two new monospecific genera of the harpacticoid family Laophontidae T. Scott, 1905 are described here. *Apistophonte wasiniensis* gen. et sp. n. was found along the Kenyan coast and *Propephonte duangitensis* gen. et sp. n. along the northern coast of Papua New Guinea. They differ from most other laophontid genera in the absence of sexual dimorphism in the endopods of the swimming legs. At first sight, both new species resemble each other very closely in habitus, integumental ornamentation, chaetotaxy of the swimming legs and absence of sexual dimorphism in the endopods. However, the detailed characteristics of A1, maxilla and male P5 show that the species are not congeneric.

The structure of the first antennular segment of *Propephonte* gen. n. suggests a close relationship with *Peltidiphonte* Gheerardyn & Fiers, 2006. The exact affinities of *Apistophonte* gen. n. however remain difficult to assess.

Keywords: Harpacticoida, Laophontidae, *Propephonte* gen. n., *Apistophonte* gen. n.

5.2. INTRODUCTION

Along the eastern coasts of Kenya and Zanzibar (Tanzania), harpacticoid copepod communities associated with dead coral substrates are being studied. As such, different types of substrate, ranging from coral sand, fine coral gravel and coral rubble to large coral fragments, have been sampled. Until now, the qualitative samples from the Kenyan coast yielded 44 species of the family Laophontidae T. Scott, 1905, including 28 which are new to science (four species have been described so far[1] (Gheerardyn *et al.* 2006a; Gheerardyn *et al.* 2006c)).

In this paper we describe one of the new Kenyan species, which is mainly characterised by the absence of sexual dimorphism in the endopodites of the natatorial legs. As this species cannot be attributed to any of the known laophontid genera, a new genus is established.

In the course of a thorough revision of the Laophontidae by Fiers (1988), numerous samples were studied from different substrates and various locations in the Atlantic, Indian and Pacific Ocean. Along the northern coast of Papua New Guinea, a coral sand and rubble sample contained a new laophontid species, which also lacks sexual dimorphism in the endopodites of the natatorial legs. Although this species closely resembles the formerly mentioned new Kenyan species, it is attributed to another new genus based on the detailed characteristics of the antennule, maxilla and male P5. Furthermore, the possible relationships of these two new genera with the other laophontid genera will be discussed.

5.3. MATERIAL AND METHODS

Along the eastern coast of Kenya, meiofauna samples were collected from various dead coral substrates (ranging from coral sand, fine coral gravel and coral rubble to large coral fragments).

[1] At the time of publication.

Prior to fixation, epifauna from coral fragments and coral rubble were rinsed off with filtered seawater over a 1 mm and a 32 μm sieve. Samples from coral gravel were obtained by decanting the coral gravel (ten times) over a 32 μm sieve. Buffered formaldehyde was added to a final concentration of 4%. In the laboratory, samples were centrifuged three times with Ludox HS40 (specific density 1.18) and finally stained with Rose Bengal.

Along the northern coast of Papua New Guinea, several samples of coral sand and coral rubble were collected following a slightly different procedure. To the sampled substrates, buffered formaldehyde was added immediately to a final concentration of 4%. In the laboratory, samples were rinsed with a jet of freshwater over a 5 mm and a 45 μm sieve, and centrifuged three times with Ludox HS40 (specific density 1.18).

Harpacticoid copepods were sorted out and counted using a Wild M5 binocular microscope and were stored in 75% ethanol. Dissected parts of the specimens were mounted in glycerine. Preparations were sealed with insulating varnish. Observations and drawings were made on a light microscope (Leica DM LS) equipped with a drawing tube. In toto specimens are stored in 75% neutralised ethanol. Type specimens are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, labelled COP). Scale bars in figures are indicated in μm.

The descriptive terminology of Huys *et al.* (1996) is adopted. Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1–P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus.

5.4. SYSTEMATICS

Family **Laophontidae T. Scott, 1905**

Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**

Genus ***Apistophonte* Gheerardyn & Fiers gen. n.**

Diagnosis

Laophontidae. Body fusiform prehensile. Rostrum prominent. Integument of cephalothorax and somites pitted. Posterodorsal margin of prosomites, urosomites and anal operculum serrate. Ventral surface of third male urosomite with several short rows of long spinules. Caudal rami cylindrical without dorsal processes. Female antennule 6-segmented; first segment short, nearly quadrate; bearing small, blunt process along the outer margin. Second segment with distinct, posteriorly directed hook along the outer margin. Syncoxa of maxilla with 3 endites. P1 with 2-segmented exopod and endopod. Swimming legs P2–P4 with 3-segmented exopods and 2-segmented endopods; without sexual dimorphism except for a curved, stronger outer spine on exp-2 of the male P3. Chaetotaxy of the ultimate exopodal segments of P2-P4: 122, 222 and 222. Endopodal lobe of female P5 reaching to middle of exopod, bearing 4 setae. Exopod of female P5 ovate, bearing 5 setae. Male P5 baseoendopod obsolete, without endopodal seta; exopod small, bearing 3 setae.

Type species – *Apistophonte wasiniensis* gen. n. sp. n., monotypy.
Etymology – The generic name is a conjunction of *apistos* (Greek meaning treacherous, perfidious) and the suffix *–phonte*, and refers to the superficial and misleading resemblance of the genus to *Propephonte* gen. n. (gender feminine).

The above diagnosis coincides with that of its only known and type species, and must, therefore, be considered tentative. A differential diagnosis is presented in the discussion.

	P2	P3	P4
Apistophonte wasiniensis	0.1.122 0.220	0.1.222 0.220	0.1.222 0.120
Propephonte duangitensis	0.1.122 0.120	0.1.222 0.120	0.1.222 0.110 (♂0.010)

***Apistophonte wasiniensis* Gheerardyn & Fiers gen. n., sp. n.** (Figures 1-4)

Type locality – Western Indian Ocean, Kenyan coast, Wasini Island (4°40'S, 39°23'E), red (terrigenous?) sediment, water depth 3–4 m.
Material – (a) From type locality: holotype ♀ dissected on 4 slides (COP4727a–d); allotype m# dissected on 3 slides (COP4728a–c); paratypes are 2 ♀♀ and 1 ♂ dissected on slides (COP4729–COP4731) and 6 ♀♀ and 4 ♂♂ preserved in 70% alcohol (COP4732); collected 28 February 2002 by M. Raes.

(b) Western Indian Ocean, Kenyan coast, Kisite Island (4°43'S, 39°22'E), coral sand, water depth 3–6: paratypes are 3 ♀♀ preserved in 70% alcohol (COP4733); collected 28 February 2002 by M. Raes.
Etymology – The specific name *wasiniensis* refers to the type locality of this species.

Description of female

Total body length 299–406 μm (n=9; average=361 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 88 μm.

Rostrum (Fig. 2A) large with straight lateral margins; broad triangular; fused to cephalothorax; with a pair of sensilla anteriorly; dorsal surface pitted.

Habitus (Fig. 1A–B). Body fusiform prehensile. Cephalothorax with parallel margins. Free prosomites slightly less wide as cephalothorax. Genital double-somite and following urosomite ventrolaterally expanded. Urosome gently tapering towards the anal somite. Second and third urosomite fused to form genital double-somite. Original division between first and second somite of genital double-somite is marked serrate dorsally.

Integument of the cephalothorax pitted; with symmetrical pattern of smooth areas; regularly ornamented with small sensilla. Surface of pleurotergites and dorsal surface of anal somite pitted entirely. Posterodorsal margin of cephalothorax smooth, of the free somites serrate. Posterolateral angles of cephalothorax slightly extended. Posterodorsal margins of cephalothorax

and free somites (except penultimate urosomite) bearing a number of small sensilla. Free prosomites and first urosomite additionally bearing 1 pair of sensilla dorsally. Anal operculum not protruding backwardly; flanked by 2 sensilla; with serrate margin.

Ventral surface (Fig. 4A) of genital double-somite smooth, except for some striae in anterior part; bearing spinular row laterally from P6 vestiges. Genital double-somite and following 2 somites bearing few spinules laterally. Ventral surface of fourth urosomite smooth; of fifth urosomite with some small spinules in posterior part; of anal somite pitted. Posteroventral margins of genital double-somite and following urosomites bearing row of slender to strong spinules.

Caudal rami (Fig. 4A, 4C) almost 1.5 times as long as wide; cylindrical with slightly convex inner margin; bearing spinules along the inner margin and several spinular rows on the ventral surface; with some small denticles and pits dorsally. Seta I, II and III inserted in distal fourth of outer margin. Seta I rudimentary. Seta IV and V not fused; seta IV pinnate, seta V naked. Seta VII inserted in the distal fourth. Antennule (Fig. 2A) 6-segmented; majority of setae long and slender. Segment 1 and 2 bearing few pits dorsally, ventral surface smooth; segment 3–6 smooth. Segment 1 short, slightly longer than wide; bearing small, blunt process along outer margin; with spinular row along inner margin. Segment 2 with distinct, posteriorly directed hook along outer margin. Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[9 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 setae.

Antenna (Fig. 2F). Allobasis bearing 2 spinular rows; with 1 short, unipinnate abexopodal seta, inserted in distal third. Exopod unisegmented and small, well developed; bearing 4 sub-equal bipinnate setae, the dorsal one being more slender and less dense pinnate. Endopod with 2 rows of spinules and 1 sub-apical frill; with following armature: 2 spines (one unipinnate) and slender seta subapically, 2 clawlike spines, 3 geniculate setae and small, slender seta apically.

Mandible (Fig. 2B). Biting edge formed by several blunt teeth and seta. Palp uniramous; endopod and exopod represented by 3 and 1 smooth seta(e), respectively. Medial seta plumose.

Maxillule (Fig. 2G). Praecoxal arthrite bearing spinular row on posterior surface; with 5 setae/spines apically; with 1 small, obliquely positioned seta along the inner margin and 2 small setae along the outer margin. Coxal endite with 1 seta and 1 curved spine. Basal endite with 2 naked setae and 1 curved spine. Endopod obsolete, represented by 3 setae. Exopod 1-segmented with 2 apical setae.

Maxilla (Fig. 2H). Syncoxa with 3 endites; with 1 row of spinules along outer margin and 2 along inner margin. Praecoxal endite small, with 1 seta. Proximal coxal endite with 1 strong, pinnate spine and 2 slender, naked setae. Distal coxal endite with 1 strong, pinnate spine and 2 slender, naked setae. Allobasis drawn out into strong, slightly curved claw; bearing 2 setae. Endopod obsolete, represented by 2 naked setae.

Maxilliped (Fig. 2E). Syncoxa with 2 spinular rows; apically bearing pinnate seta and rudimentary seta next to it. Basis with some spinules along the slightly convex outer margin. Endopod clawshaped, unarmed, with short, naked seta at base.

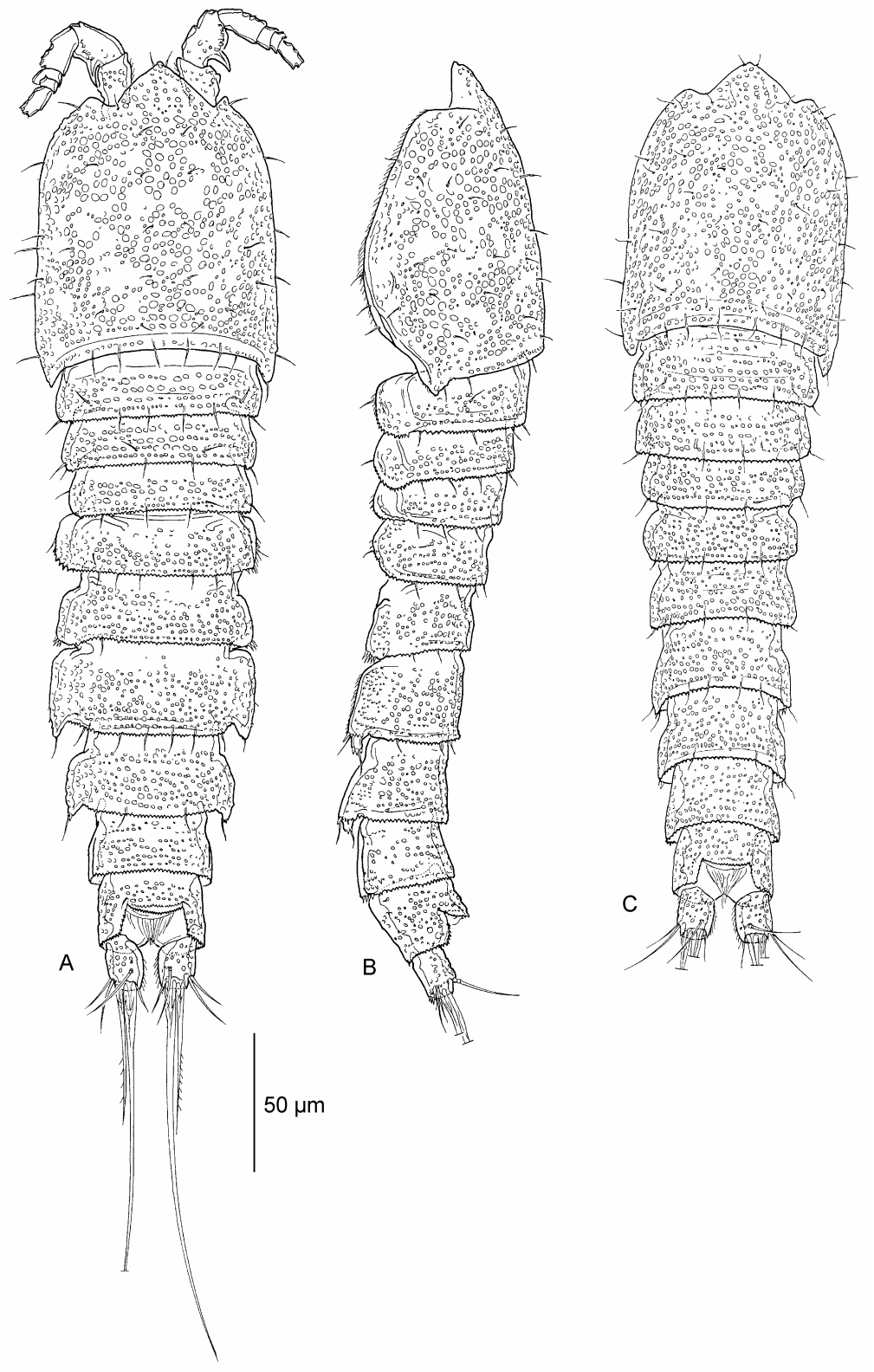

Figure 1. *Apistophonte wasiniensis* sp. n. (A) female habitus, dorsal; (B) female habitus, lateral; (C) male habitus, dorsal.

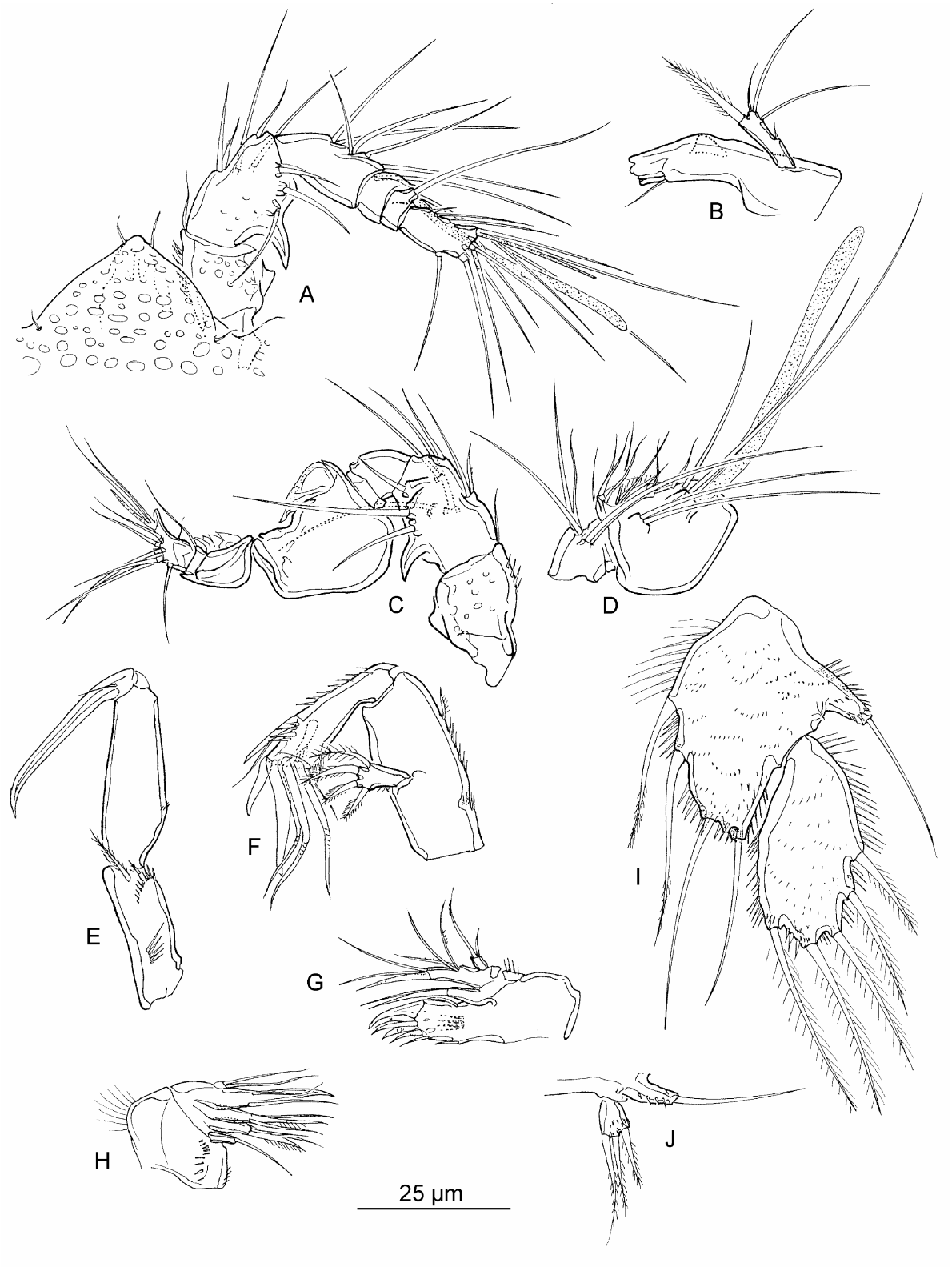

Figure 2. *Apistophonte wasiniensis* sp. n. (A) female antennule and rostrum, dorsal; (B) female mandible; (C) male antennule (armature of segments 3 to 5 omitted), dorsal; (D) male antennule (segments 3 to 5), ventral; (E) female maxilliped; (F) female antenna; (G) female maxillule; (H) female maxilla; (I) female P5, anterior; (J) male P5, anterior.

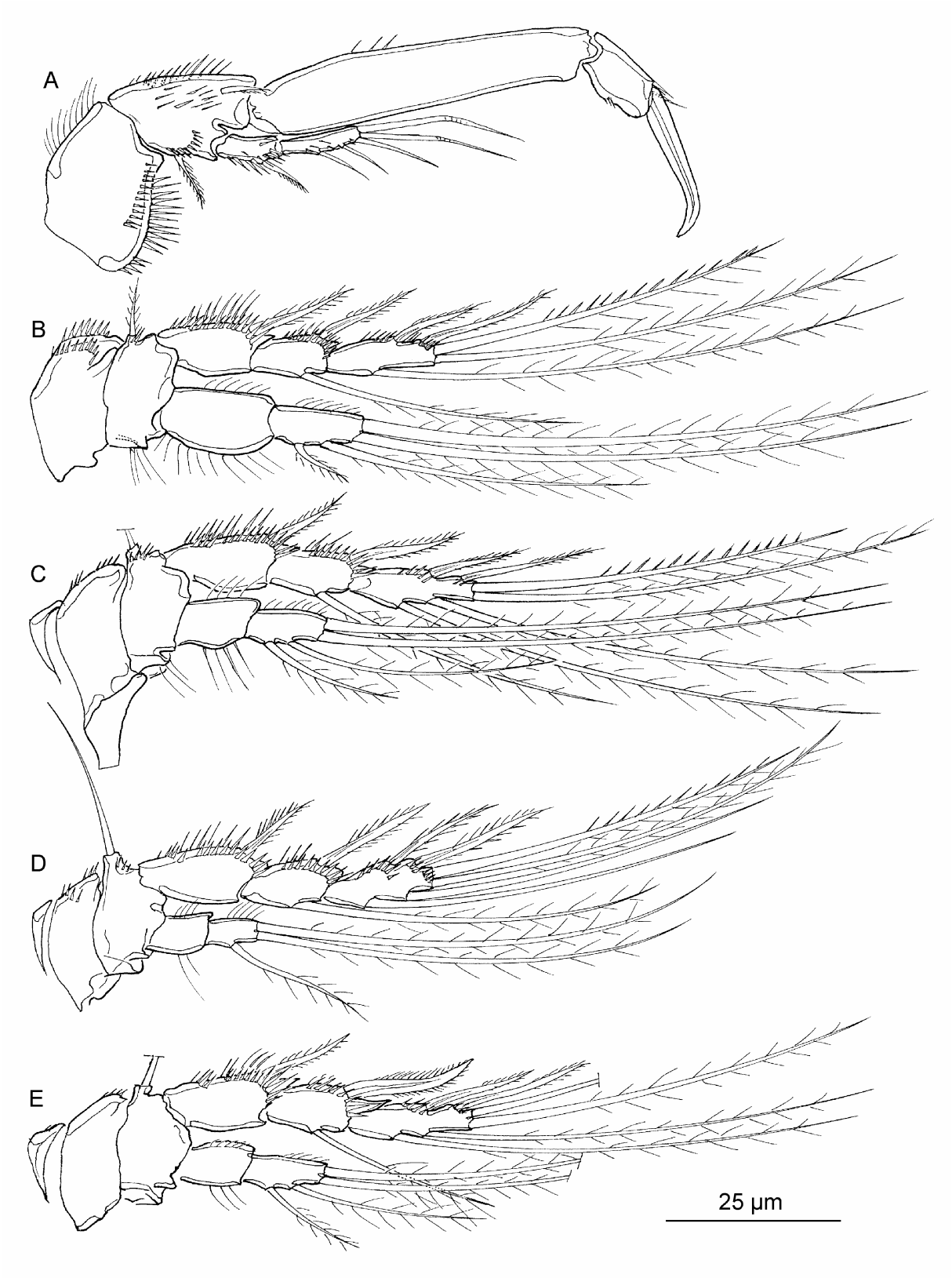

Figure 3. *Apistophonte wasiniensis* sp. n. (A) female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) male P3, anterior.

P1 (Fig. 3A). Coxa cylindrical with 1 inner and 2 outer spinular rows. Basis with 1 pinnate seta along outer margin; medial, unipinnate seta arising on anterior surface; spinules on anterior surface, along inner and outer margin. Exp-1 bearing 1 unipinnate outer seta, spinular row along the outer margin and a few spinules on the anterior surface; exp-2 bearing 3 naked outer setae and 2 geniculate apical setae, with a few spinules on the anterior surface. Enp-1 2.5 times as long as exp, with few spinules along the inner margin; enp-2 with 1 strong, smooth claw and 1 minute, naked accessory seta.

P2–P4 (Fig. 3B–D). Setal formula in table 1. Exopods 3-segmented and endopods 2-segmented. Prae-coxae small and triangular. Coxae and bases with spinules along the outer margin. Inner margin of basis in P2 and P3 with some slender long hairs. Outer margin of basis with short, pinnate (P2) or long, naked (P3–P4) seta. P2 endopod reaching to the proximal third of exp-3. P3 endopod reaching just beyond the middle of exp-2. P4 endopod slightly longer than exp-1. Segments of endopods and exopods with pattern of spinules as figured.

P5 (Fig. 2I) with separate exopod and baseoendopod; both covered anteriorly with few small spinules; the margins bearing strong and long spinules. Basal seta arising from a cylindrical setophore. Proximal setae of endopodal lobe bipinnate; sub-apical and apical seta naked. Baseoendopod reaching to middle of exopod. Exopod with ovate shape; about 2 times as long as wide; bearing 5 plumose setae.

P6 vestiges (Fig. 4A) bearing 1 seta. Copulatory pore minute, situated in middle of anterior somite.

Description of male

Total body length 280–387 μm (n=6; average=326 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 78 μm.

Habitus (Fig. 1C) as in female; except for the fully separated second and third urosomite, and the lack of ventrolateral extensions in the second to fourth urosomites (Fig. 4B). Ventral surface of third urosomite bearing several short rows of long spinules. Posteroventral margin of third urosomite with slender hairs and some long spinules near the lateral sides.

Antennule (Fig. 2C–D) 8-segmented; sub-chirocer. Segment 1 and 2 as in female. Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[5 (?)], 4-[2], 5-[10 (?) + 1 pinnate + (1 + ae)], 6-[0], 7-[1], 8-[7 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 setae.

Antenna, mouthparts and P1 as in female.

Endopods of P2–P4 as in female. Exopods of P2 and P4 as in female; except that the inner seta on exp-2 is shorter than the corresponding seta in the female (reaching not far beyond the distal margin of exp-3). P3 exopod (Fig. 3E) as in female; except for a curved, stronger outer spine on exp-2, the distal outer corner of exp-2 being more strongly developed and the inner seta on exp-2 being shorter than the corresponding seta in the female (reaching not far beyond the distal margin of exp-3).

P5 (Fig. 2J). Endopodal lobe of P5 obsolete; without a seta. Exopod small; slightly longer than wide; bearing 3 plumose setae.

P6 vestiges (Fig. 4B) asymmetrical. One vestige functional; one vestige fused to somite. Both produced into a cylindrical process bearing 1 pinnate inner and 1 naked outer seta.

Variability – Among the 12 females and 6 males studied, no variability in setal formulae was observed.

Known range – To date, *A. wasiniensis* is only known from Wasini and Kisite Islands along the Kenyan coast.

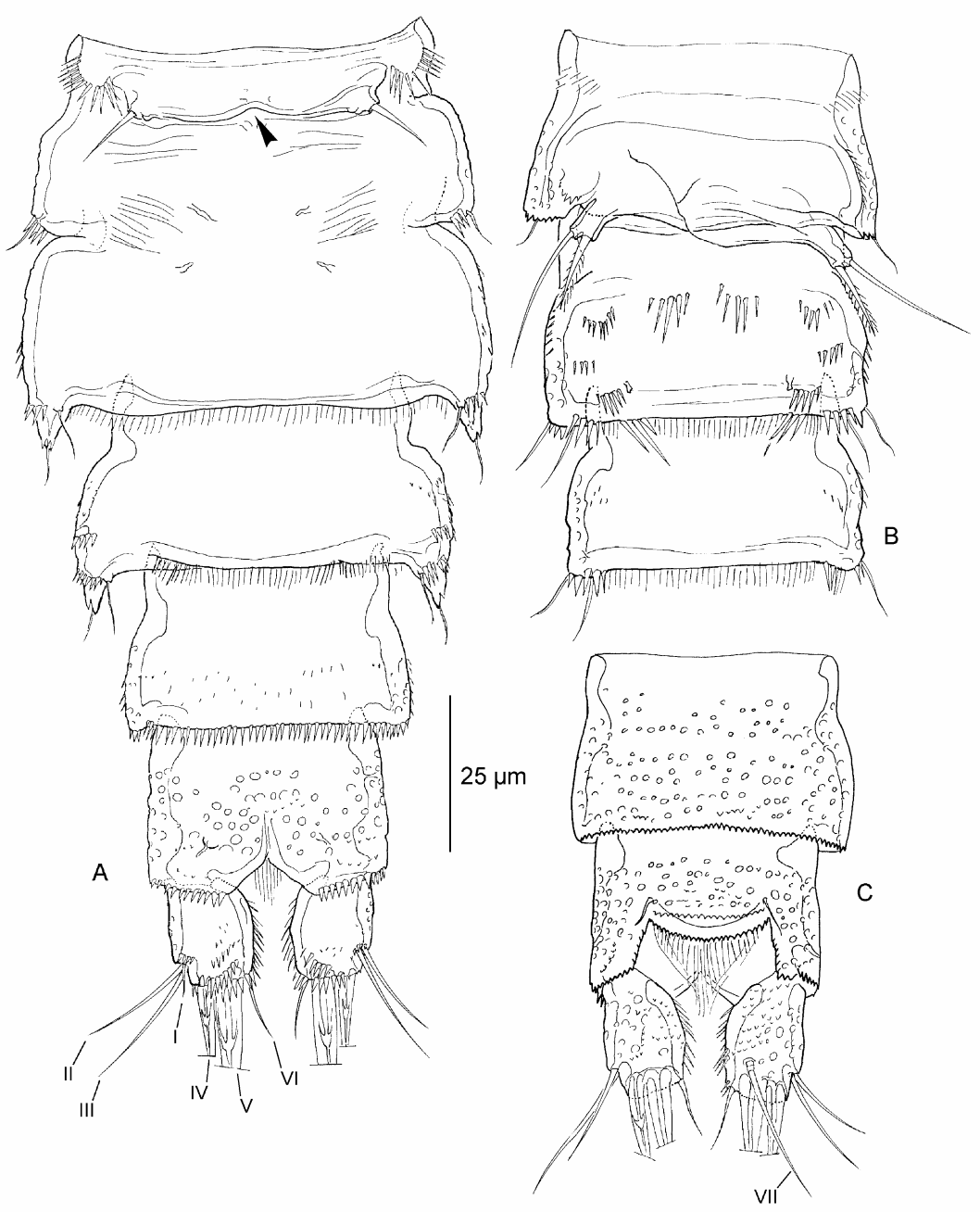

Figure 4. *Apistophonte wasiniensis* sp. n. (A) female urosome (copulatory pore arrowed), ventral; (B) male second to fourth urosomite, ventral; (C) female anal somite and caudal rami, dorsal.

Family **Laophontidae T. Scott, 1905**
Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**
Genus ***Propephonte* Gheerardyn & Fiers gen. n.**

Diagnosis

Laophontidae. Body fusiform prehensile, slightly depressed. Rostrum prominent. Integument of cephalothorax and somites pitted. Posterodorsal margin of prosomites, urosomites and anal operculum serrate. Ventral surface of third male urosomite with rows of large spinules. Caudal rami cylindrical without dorsal processes. Antennule 6-segmented; first segment distinctly elongate, with a blunt process proximally on the dorsal surface and a distinct process along the outer margin; second segment with a large, posteriorly directed hook along the outer margin. Syncoxa of maxilla with 2 endites. P1 with a 2-segmented exopod. Swimming legs P2–P4 with 3-segmented exopods and two-segmented endopods; without sexual dimorphism. Chaetotaxy of the ultimate exopodal segments of P2–P4: 122, 222 and 222. Endopodal lobe of female P5 reaching to middle of exopod, bearing 4 setae. Exopod of female P5 ovate, bearing 5 setae. Male P5 baseoendopod obsolete, with endopodal seta; exopod bearing 5 setae.

Type species – *Propephonte duangitensis* gen. n. sp. n., monotypy.
Etymology – The generic name is a conjunction of *prope* (Latin meaning close, almost) and the suffix *–phonte*, and refers to the close relationship of the genus with *Peltidiphonte* Gheerardyn and Fiers, 2006 (gender feminine).

The above diagnosis coincides with that of its only known and type species, and must, therefore, be considered tentative. A differential diagnosis is presented in the discussion.

***Propephonte duangitensis* Gheerardyn & Fiers gen. n., sp. n.** (Figures 5-9)

Type locality – Western Pacific Ocean, Papua New Guinea, Madang Province, Hansa Bay (Duangit Reef) (4°10'S, 144°53'E), coral sand and coral rubble from the east side, water depth 40–46 m.
Material – Holotype ♀ dissected on 1 slide (COP 1940); allotype ♂ dissected on 1 slide (COP 1941); paratypes are 1 ♀ dissected on 3 slides (COP4726a–c) and 1 ♂ preserved in 70% alcohol (COP 1942); all collected 28 May 1979 by J. Pierret.
Etymology – The specific name *duangitensis* refers to the type locality of this species.

Description of female

Total body length 326–350 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 88 μm.

Rostrum (Fig. 6E) strongly prominent and triangular; fused to cephalothorax; rather narrow, with slightly concave margins; tip small, slightly bifid; with pair of sensilla anteriorly; dorsal surface pitted.

Habitus (Fig. 5A, 5B). Body fusiform prehensile, slightly depressed. Cephalothorax with parallel margins, only tapering in anterior fourth. Free prosomites and first urosomite as wide as cephalothorax; second to fourth urosomites expanded ventrolaterally. Urosome gently tapering towards the anal somite. Posterolateral angles of cephalothorax lobate. Pleural areas of free prosomites well developed and rounded, bearing spinules along margin. Second and third urosomite fused to form genital double-somite. Genital double-somite with transverse serrate surface ridge dorsally and laterally, indicating original segmentation; fused ventrally.

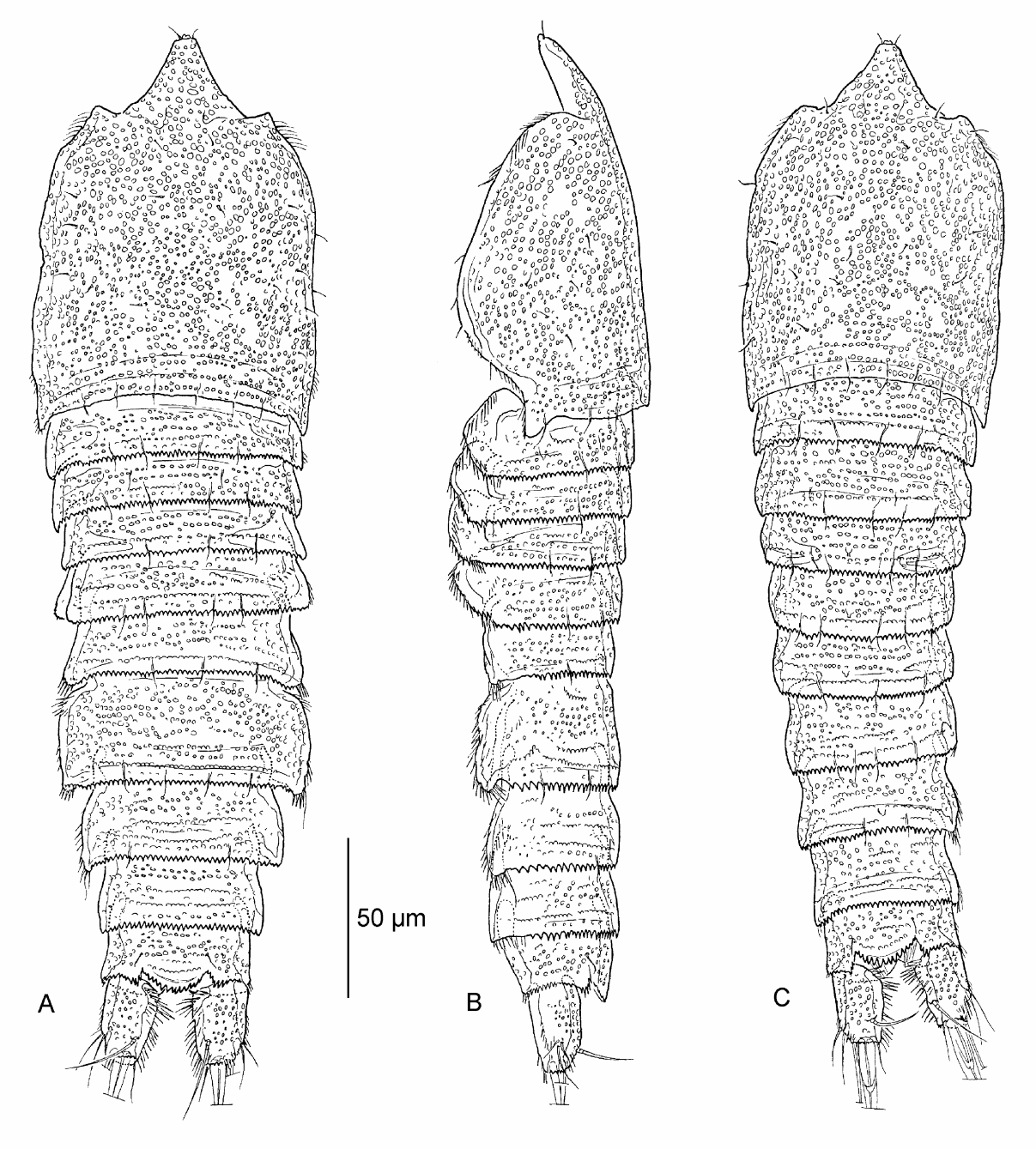

Figure 5. *Propephonte duangitensis* sp. n. (A) female habitus, dorsal; (B) female habitus, lateral; (C) male habitus, dorsal.

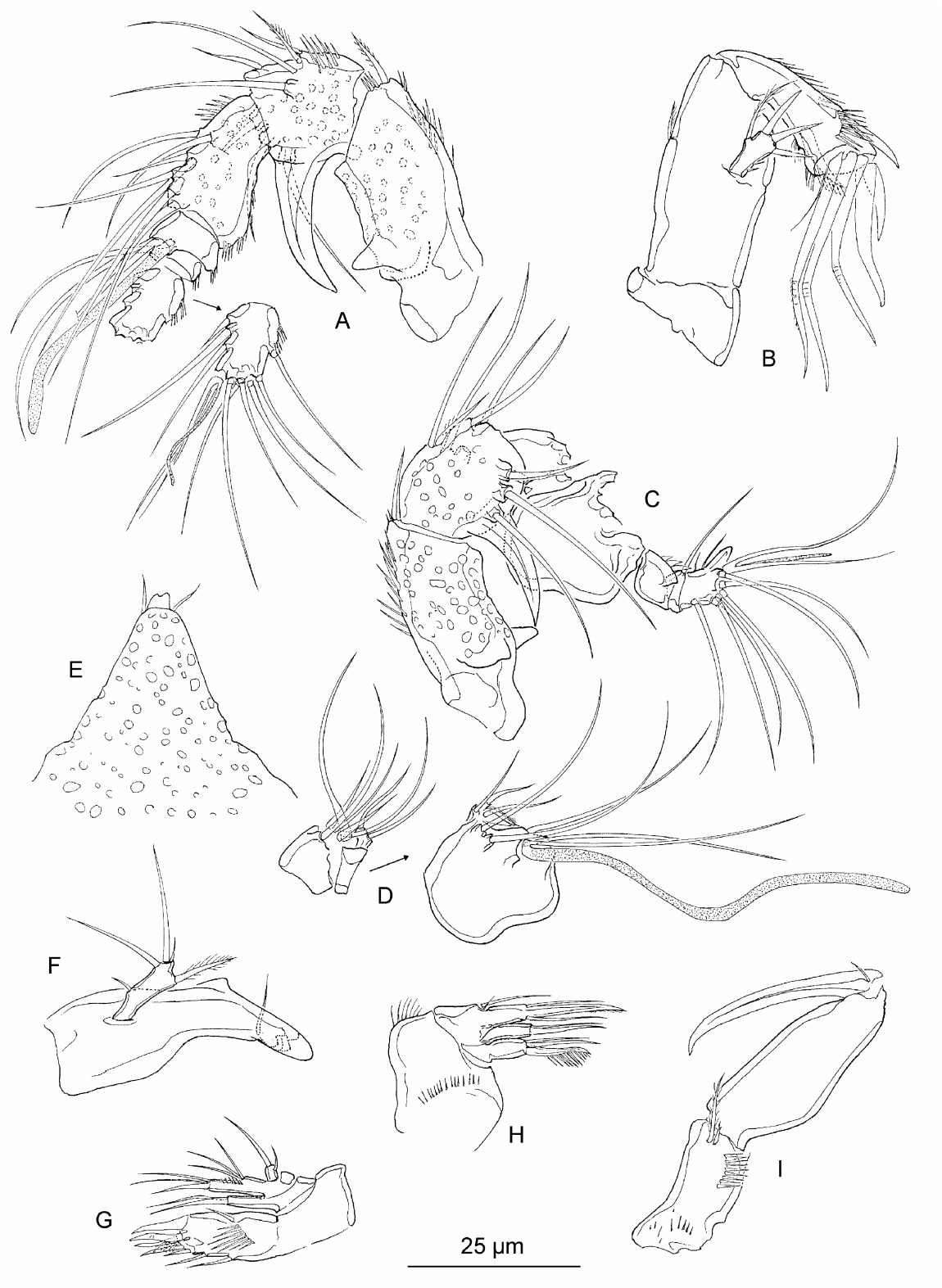

Figure 6. *Propephonte duangitensis* sp. n. A) female antennule, ventral; (B) female antenna; (C) male antennule (armature of segments 3 to 5 omitted), dorsal; (D) male antennule (segments 3 to 5), ventral; (E) female rostrum; (F) female mandible; (G) female maxillule; (H) female maxilla; (I) female maxilliped.

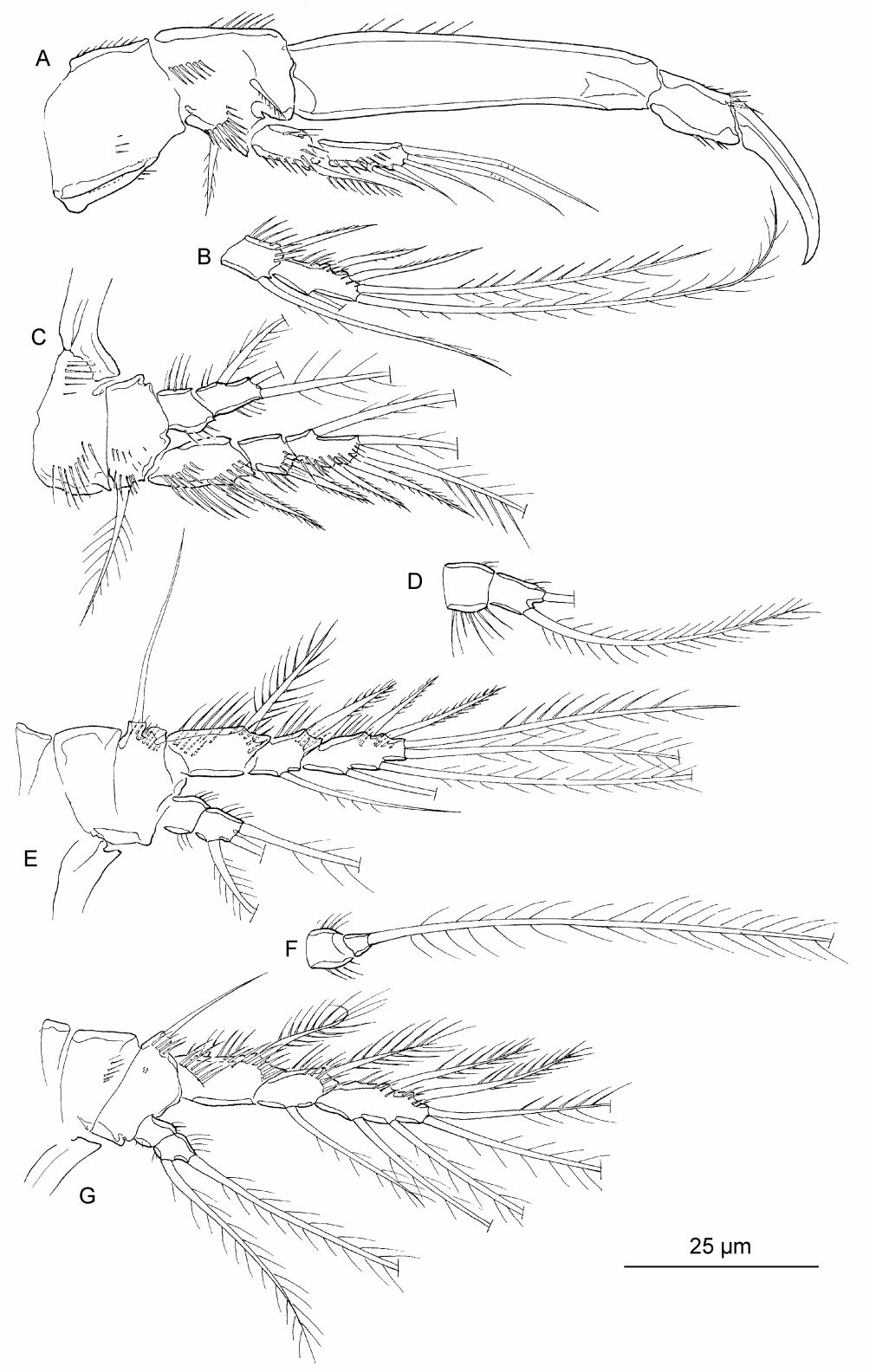

Figure 7. *Propephonte duangitensis* sp. n. (A) female P1, anterior; (B) left female P2 exp-2 and exp-3, anterior; (C) right female P2, anterior; (D) left female P2 enp, anterior; (E) right female P3, posterior; (F) left female P3 enp, posterior; (G) left female P4, anterior.

Integument of cephalothorax pitted; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites, and dorsal surface of anal somite and caudal rami entirely pitted. Rows of closely arranged pits transforming into rows of small denticles. Posterodorsal margin of cephalothorax smooth; of the free somites serrate. Posterodorsal margins of cephalothorax and free somites (except penultimate urosomite) bearing a number of small sensilla. Anal operculum well developed and slightly protruding backwardly; flanked by 2 sensilla; with serrate margin.

Ventral surface (Fig. 9A) of the genital double-somite striated anteriorly, smooth posteriorly. Ventral surface of following 2 urosomites smooth; of anal somite pitted. Posteroventral margins of genital double-somite and following urosomites bearing a row of spinules.

Caudal rami (9A–B) almost twice as long as wide; cylindrical; surface of the caudal rami without processes. Ventral surface and outer margin of the caudal rami spinulose. Inner margin slightly tapering towards the distal margin and bearing strong spinules. Seta I, II and III inserted in distal third of outer margin. Seta IV and V not fused. Seta VII inserted in the distal third.

Antennule (Fig. 6A) 6-segmented; majority of setae long and slender. Segment 1–3 pitted dorsally, smooth ventrally. Segment 4–6 smooth. Segment 1 elongate, almost 2.5 times as long as wide; dorsally with blunt process on the proximal half; outer margin bears blunt thorn proximally. Segment 2 with large, posteriorly directed hook along outer margin. Inner margin of first to third segment and outer margin of third to sixth segment with spinules. Armature formula: 1-[1 pinnate], 2-[7 + 1 pinnate], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[9 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 setae.

Antenna (Fig. 6B). Allobasis with 1 short, unipinnate abexopodal seta, inserted in distal half. Exopod unisegmented and small, but well developed; bearing three sub-equal setae apically, and one bipinnate, slender and slightly longer seta sub-apically. Endopod with 2 rows of spinules and 2 sub-apical frills; with following armature: subapically 2 spines (one is unipinnate) and a small, slender seta, apically 2 clawlike spines, 3 geniculate setae (the outermost pinnate) and 1 slender seta.

Mandible (Fig. 6F). Biting edge formed by several blunt teeth and a seta. Palp uniramous; endopod and exopod represented by 3 and 1 smooth seta(e), respectively. Medial seta plumose.

Maxillule (Fig. 6G). Praecoxal arthrite bearing a spinular row on the posterior surface; apically with 6 setae/spines; with 1 small, obliquely positioned seta along the inner and 2 slender setae along the outer margin. Coxal endite with 1 seta and 1 curved spine. Basal endite with 2 setae and 1 curved spine. Endopod obsolete, represented by 3 setae. Exopod 1-segmented with 2 apical setae.

Maxilla (Fig. 6H). Syncoxa with 2 endites; with a spinular row along the inner and along the outer margin. Praecoxal endite absent. Proximal coxal endite with 1 strong, pinnate spine and 2 slender, naked setae. Distal coxal endite with 1 curved spine and 1 slender seta. Allobasis drawn out into strong, slightly curved, distally pinnate claw; bearing 2 setae. Endopod obsolete, represented by 2 setae (one of which is very short).

Maxilliped (Fig. 6I). Syncoxa with spinular row along the outer margin and some spinules proximally; apically bearing pinnate seta and small seta next to it. Basis with slightly convex outer margin. Endopod clawshaped, unarmed, with short, naked seta at base.

P1 (Fig. 7A). Coxa and basis cylindrical, each about as long as broad; with several spinular rows. Basis with slender, plumose outer seta; inner unipinnate seta arising on anterior surface. Exopod 2-segmented, outer margins and anterior surfaces with spinules. Exp-1 with a strongly armed outer spine; exp-2 with 3 naked outer setae and 2 geniculate apical setae. Enp-1 about 2.5 times as long as exp; enp-2 with a strong, smooth claw and 1 minute, naked accessory seta.

P2–P4 (Fig. 7B–7G). Setal formula in table 1. Exopods 3-segmented and endopods 2-segmented. Prae-coxae small and triangular; devoid of integumental structures. Coxae and bases with spinules along the outer margin. Outer margin of basis with long, plumose (P2) or long, naked (P3–P4) seta. Proportional lengths of the endopods rather short; reaching to middle of exp-2 in P2, to the distal margin of exp-1 in P3 and to middle of exp-1 in P4. Outer spine of exp-1 of P3 and outer exopodal spines of P4 ornamented with slender, long spinules. Segments of endopods and exopods with pattern of spinules as figured.

P5 (Fig. 8C) with separate exopod and baseoendopod; the margins bearing long, slender spinules or stout, short spinules. Anterior surface furnished with rows of spinules. Proximal setae of endopodal lobe unipinnate; sub-apical and apical seta plumose. Baseoendopod reaching to middle of exopod. Exopod ovate shape; about 2 times as long as wide; bearing 5 plumose setae distally.

P6 vestiges (Fig. 9A) each bearing 1 small, naked seta. Copulatory pore minute, situated in middle of anterior somite.

Description of male

Total body length 309–350 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 80 μm.

Habitus (Fig. 5C). More slender than female; especially with respect to the urosome. Second and third urosomite fully separated. Ventrolateral extensions of second to fourth urosomite are absent. Ventral surface of third urosomite with 2 rows of long spinules; anterior one along the entire surface, posterior one with a large gap in the middle (Fig. 9C).

Antennule (Fig. 6C–D) 8-segmented; sub-chirocer. Segment 1 and 2 as in female. Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[6], 4-[2], 5-[9 (?) + (1 + ae)], 6-[0], 7-[1], 8-[8 + acrothek]. Apical acrothek consisting of a small aesthetasc fused basally to 2 setae.

Antenna, mouthparts and P1 as in female.

Swimming legs P2–P4 as in female (Fig. 8A–B), except enp-2 of P4 has lost the inner seta.

P5 (Fig. 8D) pair of legs medially fused. Endopodal lobe of P5 obsolete; bearing 1 pinnate seta. Exopodite oblong; bearing 5 setae and a row of spinules along the outer margin.

P6 vestiges (Fig. 9C) asymmetrical. 1 vestige functional; 1 vestige fused to somite; outer distal corner with 1 pinnate inner and 1 naked outer seta, each on small pedestal.

Variability – The female holotype has a left P2 enp (Fig. 7D) with only one apical seta, a right P2 exp-2 (Fig. 7C) without an inner seta and a left P3 enp (Fig. 7F) with a very small second segment, bearing only one seta. The allotype bears only two setae on the right endopod of P3, which contrasts with the other paratypes and the left endopod of the same specimen.
Known range – To date, *P. duangitensis* is known from the type locality only.

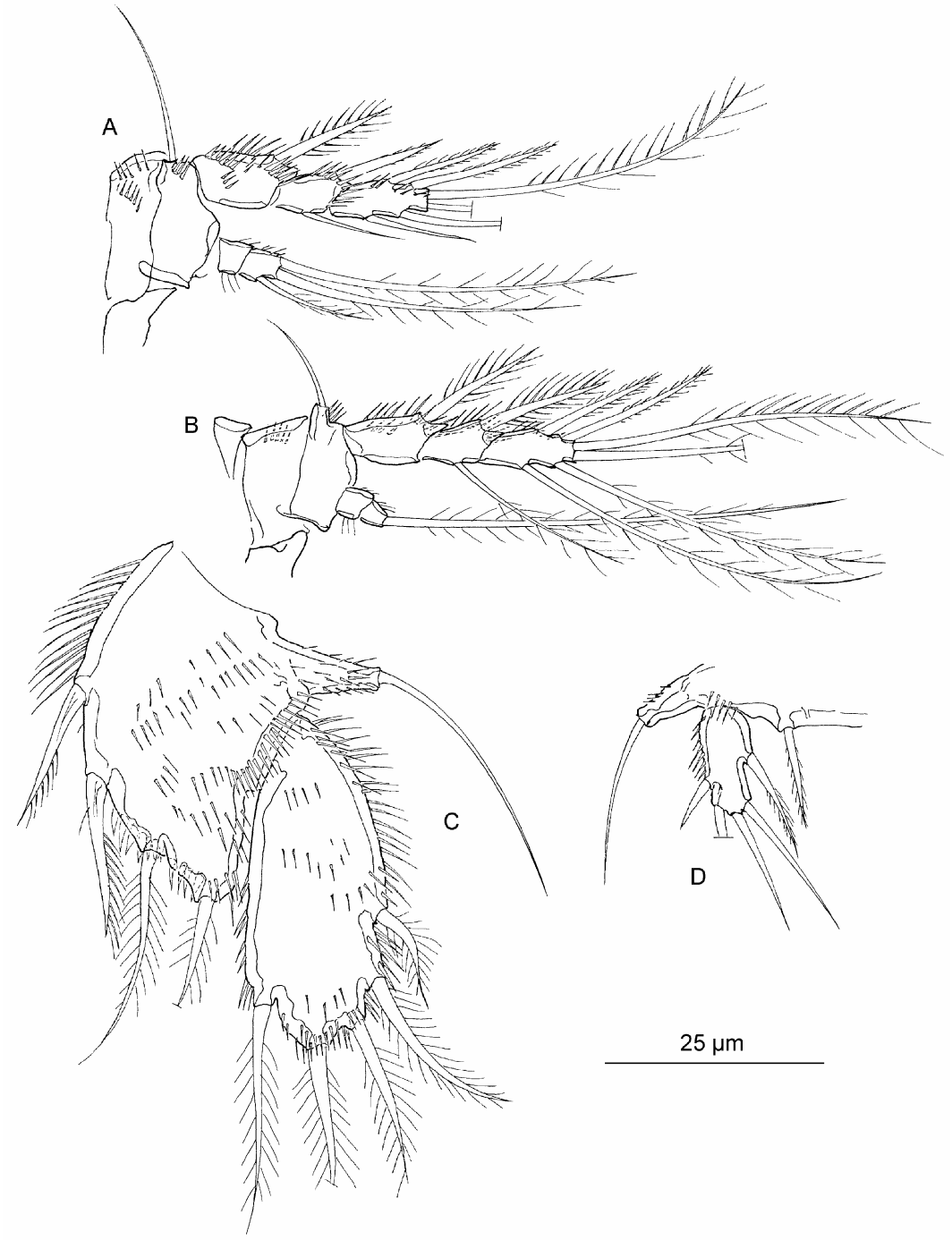

Figure 8. *Propephonte duangitensis* sp. n. (A) male P3, anterior; (B) male P4, posterior; (C) female P5, anterior; (D) male P5, anterior.

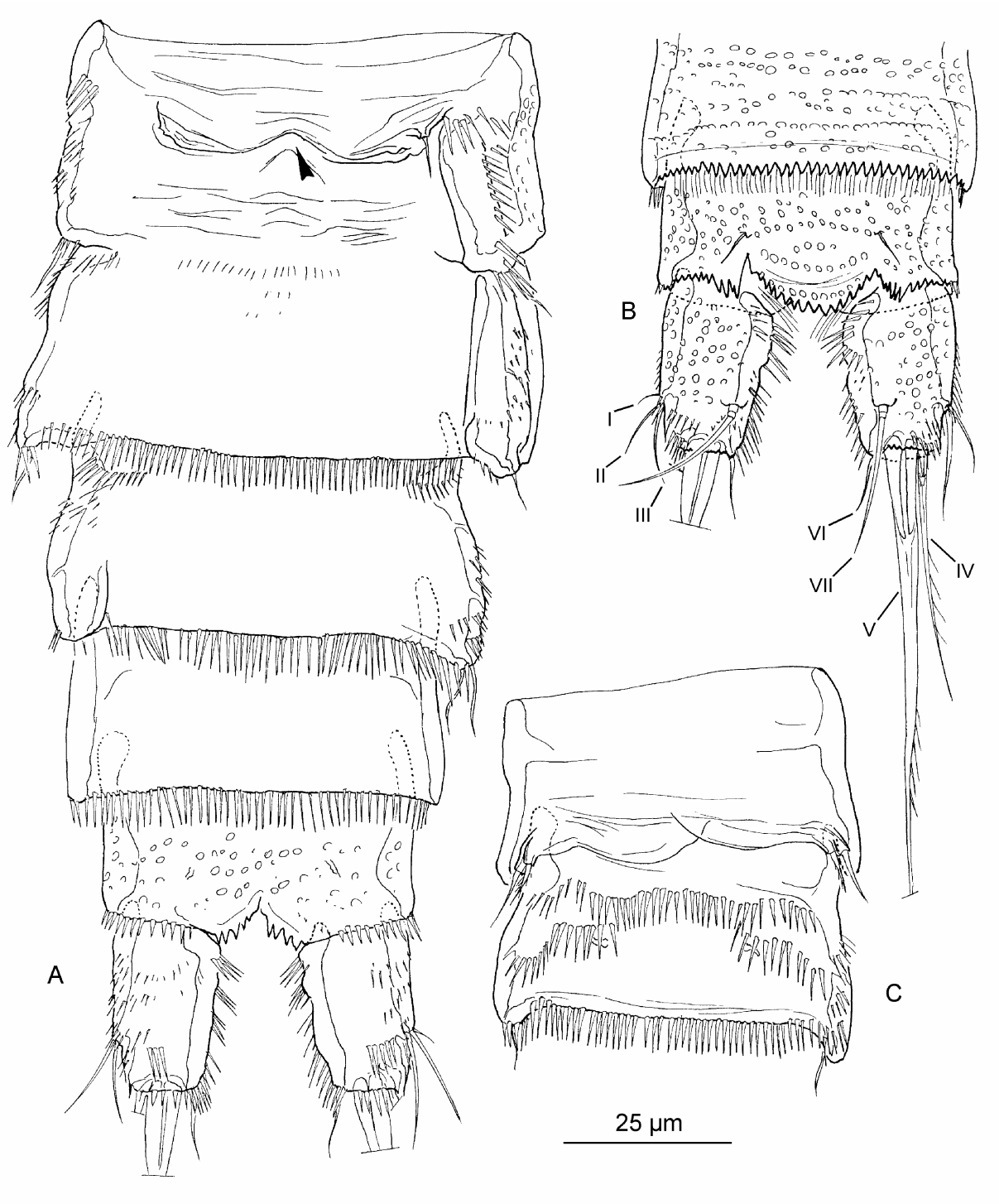

Figure 9. *Propephonte duangitensis* sp. n. (A) female urosome (copulatory pore arrowed), ventral; (B) female anal somite and caudal rami, dorsal; (C) male second and third urosomite, ventral.

5.5. DISCUSSION

Apistophonte gen. n. and *Propephonte* gen. n. are both placed in the family Laophontidae and more specifically in the subfamily Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000 based on the following synapomorphies as defined by Huys & Lee (2000): male antennule with up to three segments distal to geniculation, proximal aesthetasc fused to one seta, mandible uniramous, maxilliped with maximum two setae on syncoxa, P1 enp-1 without inner seta, P2 enp-2 without outer spine, proximal outer setae of female P5 exopod with distinctly separated insertion sites and absence of cup-shaped transformed pores on legs or somites. Both genera differ from most other laophontid genera in the absence of sexual dimorphism in the P2–P4 endopods. In the superfamily of Laophontoidea T. Scott, a particularly robust character is the presence of sexual dimorphism in the P3 endopod (Huys, 1990). The male apophysis of the Laophontoidea can be unequivocally defined as the homologue of the female outer spine on the distal endopodal segment of P3. As a consequence of the loss of this outer spine, a sexually dimorphic apophysis on the male P3 endopod is absent, as stated by Huys (1990). This loss has occurred independently in several lineages in the Laophontidae as shown by e.g. *Echinolaophonte tetracheir* Mielke, 1981, *Lipomelum* Fiers, 1986, *Loureirophonte* Jakobi, 1953, *Paralaophonte aenigmaticum* Wells, Hicks & Coull, 1982 and *Peltidiphonte* Gheerardyn & Fiers, 2006.

At first sight, *Apistophonte wasiniensis* sp. n. and *Propephonte duangitensis* sp. n. resemble each other very closely because of their comparable habitus, pitted integument, absence of sexual dimorphism in the P2–P4 endopods, chaetotaxy of the swimming legs and similar female P5. Closer examination of A1, mouthparts, male P5 and proportions of the endopods of the swimming legs nevertheless reveals that these two new species are not congeneric and furthermore cannot be included in any of the known genera.

The first antennular segment in *Propephonte* gen. n. is elongate (almost 2.5 times as long as wide), and bears a distinct process proximally on the dorsal surface and a blunt thorn along the outer margin. This particular structure of the first antennular segment indicates a close relationship with the genus *Peltidiphonte*. Furthermore, the fifth pereiopods of male and female of both genera are similar in shape and setation, up to the shape of the setae. *Propephonte* gen. n. and *Peltidiphonte* have both lost the praecoxal endite on the maxilla and the outer spine on the P3 endopod. Based on these shared characteristics, we assume that *Propephonte* gen. n. and *Peltidiphonte* belong to the same lineage in which *Peltidiphonte* became adapted to an epibenthic life style by becoming dorsoventrally flattened. The laterally extended pleurotergites of the prosomites and the broad and wing-like urosomites are a distinct apomorphy for the latter genus. *Propephonte* gen. n. shows a typical fusiform prehensile, but slightly depressed, habitus. As *Peltidiphonte* has a three-segmented P1 exopod and three outer spines on the ultimate exopodal segments of the swimming legs, the two-segmented P1 exopod and the reduced chaetotaxy of the last exopodal segments are apomorphies supporting the establishment of *Propephonte* gen. n. The male of *Propephonte duangitensis* sp. n. furthermore has lost the inner seta on the second endopodal segment of P4.

As shown by the structure of A1, maxilla and male and female P5, it is plausible that *Indolaophonte* Cottarelli, Saporito & Puccetti, 1986 and *Langia* Wells & Rao, 1987 are more derived genera within this lineage, wherein the setation and segmentation of the swimming legs became more reduced as an adaptation to the interstitial life style. The distal process on the caudal ramus (being homologous to a posterior outgrowth of the outer distal corner) is a distinct synapomorphy for these two genera. The first antennular segment in both genera is elongate and bears a distinct process along the outer margin. However, a process on the dorsal surface is not drawn nor mentioned in the text of the original descriptions of the two species of *Indolaophonte* (Cottarelli *et al.*, 1986; Cottarelli & Puccetti 1988). An as yet undescribed species of *Indolaophonte* conversely shows the presence of this dorsal process (personal observation by F.F.). The detailed structure of the antennule in the monospecific genus *Langia* is rather unclear in the drawing by Wells & Rao (1987). The outer process on the first segment seems to be confluent with a dorsal elevation. In a redescription of *Langia maculata* Wells & Rao, 1987 by Mielke (1997), a dorsal process also appears to be absent. However, additional material from the northern coast of Papua New Guinea and the eastern coast of Bali clearly shows the presence of a dorsal process on the first antennular segment of this species (personal observation by F.F.).

It is worth mentioning that *Propephonte duangitensis* sp. n. was encountered in exactly the same sample as *Peltidiphonte furcata* Gheerardyn & Fiers, 2006 illustrating both species occur in the same type of habitat.

Contrary to the above-mentioned genera, the first antennular segment in *Apistophonte* gen. n. is nearly quadrate (only slightly longer than wide) and only bears a small process along the outer margin. Other characteristics, such as the proportional size of the endopods (being distinctly longer than the respective ones in *Propephonte* gen. n. and *Peltidiphonte*) and the presence of a praecoxal endite on the maxilla, also show that *Apistophonte wasiniensis* gen. n. sp. n. cannot be included in *Propephonte* gen. n. Although the female P5 is similar in shape and setation to the condition in *Propephonte* and *Peltidiphonte*, the shapes of the endopodal setae are however clearly different. In *Apistophonte*, the endopodal part of the female P5 bears two inner bipinnate, slender setae, and a sub-apical and apical naked seta. In *Propephonte* and all eight species of *Peltidiphonte*, the two inner elements are stout and unipinnate, while the sub-apical and apical seta are plumose. It is supposed that *Apistophonte* gen. n. branched off from a different stock than the lineage grouping *Propephonte* gen. n. and *Peltidiphonte*. As a consequence, the two-segmented P1 exopod and the reduced chaetotaxy of the last exopodal segments in *Apistophonte* gen. n. and *Propephonte* gen. n. have to be considered a result of convergence. *Apistophonte* gen. n. is distinguished from the other genera of the family by the following combination of character states: the absence of sexual dimorphism in the endopods of the swimming legs, the strongly reduced male P5 (having lost the endopodal seta and bearing only three setae on the small exopod), the presence of a curved, stronger outer spine on exp-2 of the male P3 and the loss of the outer spine on the endopodite of P3. In our opinion, these features seem to be sufficient to justify the institution of the new genus.

The loss of the outer spine on the second endopodal segment of P3 could be a synapomorphy grouping *Apistophonte* gen. n., *Propephonte* gen. n. and *Peltidiphonte*. The absence of sexual dimorphism in the P2–P4 endopods however is not unique within the Laophontidae, as it has been lost several times. Therefore, it is difficult to elucidate the possible relationships of *Apistophonte* gen. n. with other genera of the family.

5.6. ACKNOWLEDGEMENTS

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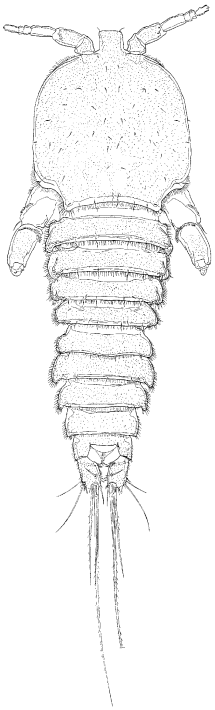
CHAPTER 6

Paralaophonte harpagone sp. n. (Copepoda: Harpacticoida), a laophontid with an extremely specialised maxilliped



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6.1. ABSTRACT

A new species of *Paralaophonte* Lang, 1944 is described from the coast of Kenya. The new species does not show any sexual dimorphism in the endopodite of P3 nor in the exopodites of P2 to P4. However, it is a true representative of the genus *Paralaophonte* by the typical sexually dimorph P2 endopodite with its modified distal inner seta on the second endopodal segment. The most distinguishing feature of the new species is the robust, enlarged and specialised maxilliped, present in both sexes. The maxilliped is similar in robustness and position to the highly specialised maxilliped of the genus *Namakosiramia* Ho & Perkins, 1977, of which the two members exist as ectoparasites on holothurians. We can only speculate whether the specialised maxilliped of *Paralaophonte harpagone* sp. n. is an adaptation to live as an associate of another invertebrate.

Keywords: Laophontidae, *Paralaophonte harpagone* sp. n., specialised maxilliped

6.2. INTRODUCTION

The harpacticoid family Laophontidae T. Scott, 1905 is a large and heterogeneous group, at present including 63 genera (Huys & Lee 2000; Gheerardyn *et al.*, 2006a). Throughout the family, the maxilliped shows little variation compared to the maxilliped of the type species *Laophonte cornuta* Philippi, 1840. This type of maxilliped consists of a cylindrical syncoxa bearing up to 3 setae, a basis with a straight palmar and a convex outer margin and an endopodal claw bearing one accessory seta at base. The maxillipeds are typically inserted close to each other on both sides of the longitudinal axis of the copepod. However, dimensions and firmness of the composing elements, i.e. syncoxa, basis and endopodal claw, can vary.

Nearly all members of the subfamily Esolinae Huys & Lee, 2000 have a slender maxilliped with an elongate basis and endopodal claw. Species of *Echinolaophonte* Nicholls, 1941 are also characterised by a long and slender maxilliped. The two species of the closely related genus *Xanthilaophonte* Fiers, 1991, living in close association with decapods (Fiers, 1991a), have stronger built, robust maxillipeds. While in *Robustunguis* Fiers, 1992 the strong and large prehensile first leg grasps the bristles of its decapod host (Fiers, 1992), this function may mainly be done by the strong maxilliped in *Xanthilaophonte*. A well developed and strongly prehensile maxilliped permits the two species of *Mictyricola* Nicholls, 1957 to live commensally with land crabs (Nicholls, 1957). Large and strongly built maxillipeds are also present in *Raptolaophonte ardua* Cottarelli & Forniz, 1989 and *Harrietella simulans* (T. Scott, 1894), the latter living as an associate of wood-infesting Isopoda of the genus *Limnoria* (Pinkster, 1968). A very strongly built maxilliped is encountered in the highly specialised members of the laophontid genus *Namakosiramia* Ho and Perkins, 1977. The two species of this genus live as ectoparasites on holothurians in which their maxilliped, P1 and P2 form powerful anchoring appendages to adhere to the host (Ho & Perkins, 1977; Huys, 1988a).

A new species of *Paralaophonte* Lang, 1944 is described here. Its most distinguishing feature is the particular robust, backwardly directed maxilliped, apart from the absence of sexual dimorphism in the endopodite of P3 and the exopodites of P2 to P4.

6.3. MATERIAL AND METHODS

Meiofauna samples were collected from dead coral fragments along the Kenyan coast. Epifauna from coral fragments and coral rubble was rinsed off over a 1 mm and a 32 μm sieve. Shortly after collecting, a buffered formaldehyde solution was added to a final concentration of 4%.

In the laboratory, samples were rinsed with a jet of freshwater over a 1 mm sieve, then decanted ten times over a 32 μm sieve, subsequently centrifuged three times with Ludox HS40 (specific density 1.18) and finally stained with Rose Bengal. Harpacticoid copepods were sorted out and counted using a Wild M5 binocular and were stored in 75% ethanol.

Observations and drawings were made from whole and dissected specimens mounted in glycerine, using a light microscope (Leica DM LS) equipped with a drawing tube. Preparations were sealed with insulating varnish. In toto specimens were stored in 75% ethanol. Type specimens are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, labelled COP). Scale bars in figures are indicated in μm.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus.

6.4. SYSTEMATICS

Family **Laophontidae T. Scott, 1905**

Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**

Genus ***Paralaophonte* Lang, 1944**

***Paralaophonte harpagone* Gheerardyn, Fiers, Vincx & De Troch sp. n.** (Figures 1-4)

Type locality – Western Indian Ocean, Kenyan coast, in front of village Kurwitu (3° 47' S, 39° 49' E), collected from dead coral fragments, water depth less than 1 m.

Material – (a) From type locality: holotype ♀ on 1 slide (COP 4714); allotype ♂ dissected on 3 slides (COP 4715a-c); paratypes are 2 ♀♀ and 2 ♂♂ dissected on slides (COP 4716 – COP 4719), and 4 ♀♀, 4 ♂♂, 2 CII, 1 CIII, 2 CIV and 1 ♀ CV (COP 4720) preserved in 70% alcohol; all collected 26 February 2002 by M. Raes.

(b) Western Indian Ocean, Kenyan coast, Watamu Marine Park (3° 21' S, 40° 1' E), dead coral fragments, water depth 2 to 3 m. – paratype is 1 ♀ (COP 4721) preserved in 70% alcohol; collected 27 February 2002 by M. Raes.

Etymology – The specific name is derived from the Latin *harpago* (grappling hook) (*harpagone* is the ablative form) and refers to the large maxilliped.

Description of female

Total body length 356 – 415 μm (n = 7; average = 395 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at cephalothorax just in front of insertion of Mxp: 137 μm.

Rostrum (Fig. 2G) fused to cephalothorax, slightly longer than wide, with parallel margins and truncated at the tip; with a pair of sensillae anteriorly; dorsal surface clothed with minute spinules.

Habitus (Fig. 1A,B). Body depressed. Cephalothorax as long as broad, rounded anteriorly, posterolateral angles concave before insertion of Mxp. Largest width just in front of insertion of Mxp. Free prosomites and following two urosomites gradually tapering posteriorly; third urosomite slightly wider than second urosomite; following urosomites gradually tapering posteriorly. Pleural areas of free prosomites well developed and rounded with lobate posterolateral angles. Second and third urosomite fused to form genital double-somite. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation; fused ventrally.

Integument of cephalothorax, pleurotergites of prosomites and urosomites, and dorsal surface of anal somite and caudal rami clothed with minute spinules. Spinules are somewhat larger in the pleural areas. Cephalothorax regularly ornamented with small sensillae. Posterodorsal margins of cephalothorax and free somites smooth with a number of small sensillae (not in the penultimate urosomite). Lateral and posterodorsal margins of cephalothorax, free prosomites and urosomites clothed with slender spinules which are stronger in the pleural areas. Free prosomites and first urosomite bearing some stout spinules near transition of tergital and pleural areas.

Ventral surface (Fig. 4B) of the genital double-somite smooth, except for some median striae. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following urosomites with some spinules laterally, smooth medially. Ventral surface of caudal rami smooth. Posteroventral margins of genital double-somite and of following urosomites bearing a row of strong spinules.

Caudal rami (Fig. 4A) 1.5 times as long as wide; cylindrical with straight inner and outer margin. Inner margin bearing two transverse rows of long spinules. Seta I, II and III inserted in distal fourth of outer margin, seta VII in distal third. Seta IV and V not fused, both pinnate; all other setae naked.

Antennule (Fig. 2A) six-segmented; majority of setae long and slender; segment I to III dorsally clothed with minute spinules; segment IV to VI smooth. Segment I with spinular rows on inner, outer and distal margins. Segment II bearing a small blunt process along the outer margin, and spinular rows along inner and outer margin. Segment III with some long spinules along inner margin. Armature formula: I-1, II-8, III-7, IV-2 + ae, V-1, VI-11 + ae.

Antenna (Fig. 2H). Coxa with 1 spinular row. Allobasis with 1 short and unipinnate abexopodal seta. Exp unisegmented and small, bearing 4 sub-equal bipinnate setae (2 laterally, 2

apically). Enp bearing 4 spinular rows; with following armature: subapically 2 spines and a slender seta, apically 2 strong spines, 3 geniculate setae, and 1 minute seta.

Mandible (Fig. 2D). Biting edge formed by several blunt teeth and a seta. Palp uniramous; medial seta plumose, 3 apical setae smooth.

Maxillule (Fig. 2E). Praecoxa with a rather short arthrite; bearing a spinular row on posterior surface and 1 seta on anterior surface; medial margin furnished with 8 setae/spines. Coxal endite with 1 seta and 1 curved, pinnate spine. Basal endite with 2 naked setae and 1 curved, pinnate spine. Endopod obsolete, represented by 3 setae. Exopod 1-segmented with 2 apical setae.

Maxilla (Fig. 2F). Syncoxa with 3 endites; with 1 row of spinules along outer and 1 along inner margin. Praecoxal endite small, with 1 seta. Both coxal endites with 1 strong, pinnate spine and 2 slender, naked setae. Allobasis drawn out into strong, slightly curved, distally pinnate claw; bearing 2 pinnate setae and 1 small, naked seta. Endopod obsolete, represented by 2 naked setae.

Maxilliped (Fig. 2K) robust; held laterally from the body, backwardly directed. Syncoxa robust; with 2 spinular rows and 1 naked seta. Basis robust; with 1 transverse row of spinules along outer margin; outer surface clothed with minute spinules; distal third of palmar margin markedly concave, bordered with 1 transverse row of stout spinules along the strongly sclerotised integument. Endopod strongly sclerotised, claw-shaped, unarmed and short (length equals a third of the length of the basis); with short seta at base.

P1 (Fig. 3A). Coxa cylindrical; with spinules along outer margin. Basis with 1 pinnate seta along outer margin; medial seta arising in middle of anterior surface; spinules along inner and outer margin; 1 anterior tube pore near articulation with coxa. Exp-1 with 1 unipinnate outer seta; exp-2 2 times as long as exp-1, with 2 naked outer spines and 2 geniculate apical setae. Enp-1 2 times as long as exp; with spinules along inner margin. Enp-2 with spinules along outer margin; with 1 strong, smooth claw and 1 minute, naked accessory seta.

P2-P4 (Fig. 3B-D). Setal formula in table 1. Exopodites 3-segmented and endopodites 2-segmented. Prae-coxae triangular with an outer row of small spinules. Coxae with rows of long spinules along outer margin. Bases with a spinular row near the insertion place of the long, slender, pinnate (P2) or naked (P3-P4) basal seta; and 1 anterior tube pore. Segments of endopodites and exopodites with pattern of spinules as figured.

P5 (Fig. 2I) with separate exopod and baseoendopod; both anteriorly covered with spinules; margin of endopodal lobe with strong spinules. Basal seta arising from a cylindrical setophore with a tube pore proximally. Proximal spines of endopodal lobe strong and bipinnate; sub-apical and apical seta plumose. Exopod reaching far beyond the baseoendopod; rounded; slightly longer than wide; bearing 4 setae (2 plumose, 2 naked), closely set in distal region.

P6 vestige (Fig. 4B) bearing 1 seta.

Description of male

Total body length 349 – 379 μm (n = 7; average = 366 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at cephalothorax just in front of insertion of Mxp: 114 μm.

Habitus as in female. Second and third urosomites fully separated (Fig. 4C). Ventral surface of third urosomite with several rows of spinules laterally; smooth medially.

Antennule (Fig. 2B,C) 7-segmented; sub-chirocer. Segment I and II as in female. Armature formula: I-1, II-9, III-7, IV-2, V-11(?) + ae, VI-1, VII-10 + ae.

Mouthparts, P1, P3 and P4 as in female.

P2 (Fig. 3E). Exopod as in female. Distal inner seta of enp-2 strongly built in proximal half; with long hairs proximally, strong spinules medially and plumose distally.

P5 (Fig. 2J). Endopodal lobe of P5 obsolete; bearing 1 plumose seta with some spinules medially to it, spinules absent at opposite endopodal lobe. Basal part with a naked seta on a setophore, clothed with spinules. Exopodite oblong; about 2 times longer than wide; bearing 5 setae: 1 outer, 1 apical and 3 inner setae (outer seta smooth, other setae plumose). Outer margin and anterior surface with spinules.

P6 vestiges (Fig. 4C) asymmetrical. One vestige functional; one vestige fused to somite; outer distal corner with 1 plumose inner and 1 naked outer seta, each on a small pedestal.

Copepodids

Copepodid stages CII to CV (CI not found) all have a robust maxilliped; held laterally from the body (Fig. 1C, 2L). The syncoxal seta appears in the third copepodid stage.

Variability – Whereas females show almost no variability, males have a variable P2 exopodal armature. Most males have a left or right P2 with only 2 outer spines on exp-3 (Fig. 4D), the opposite leg consistently has a normal setal formula with 3 outer spines. The allotype has an aberrant P3 enp (1.220) (Fig. 4E) on the right side; one male paratype has a left and right P3 with an aberrant exopodal armature (0.1.122); one other male paratype has 6 exopodal setae on the right P5 (Fig. 4F).

	P2	P3	P4
Exp	0.1.123	0.1.223	0.1.222
Enp	0.220	0.220	0.120

Table 1. *Paralaophonte harpagone* sp. n. Swimming leg setal formula.

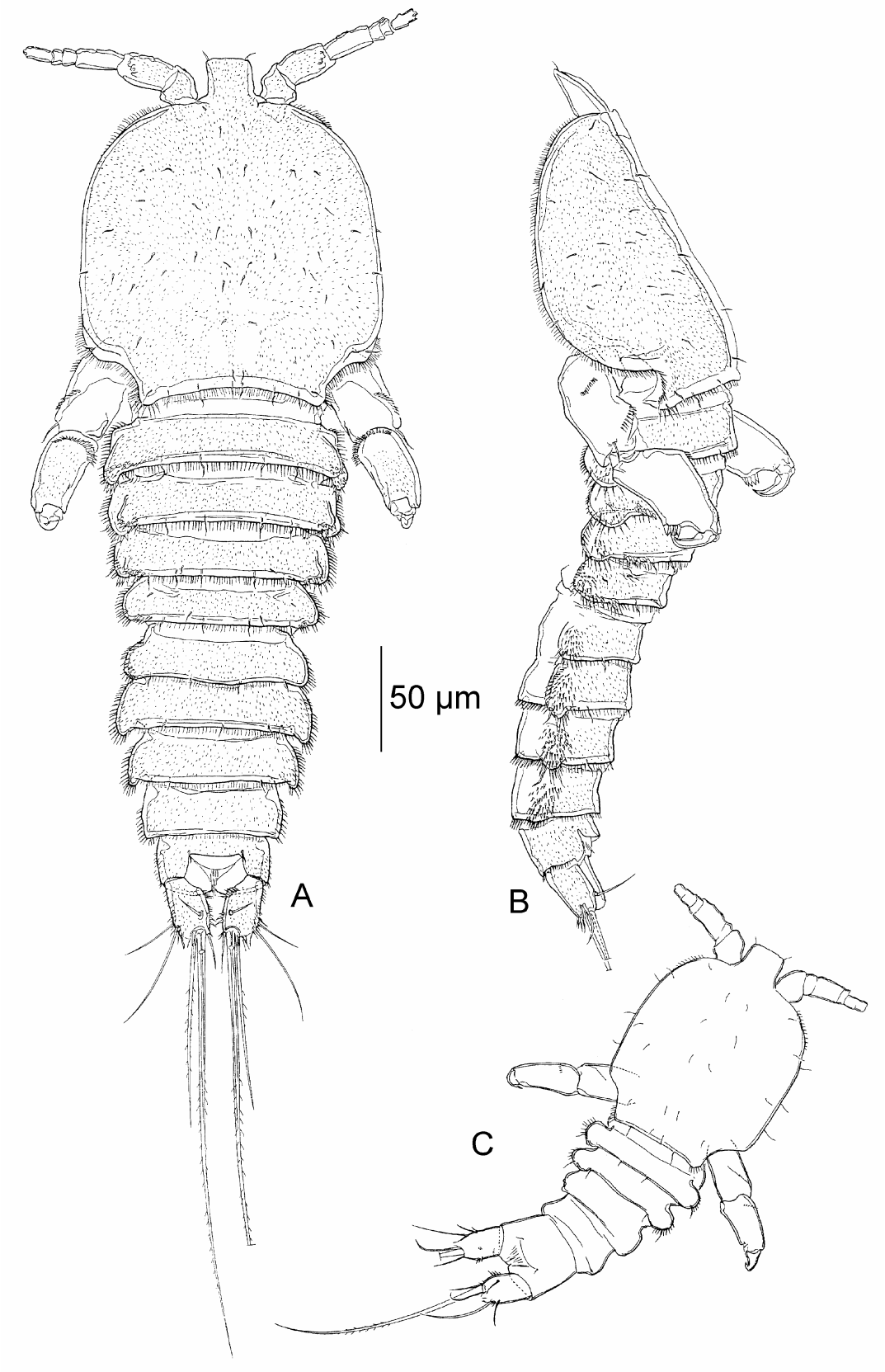

Figure 1. *Paralaophonte harpagone* sp. n. (A) female habitus, dorsal; (B) female habitus, lateral; (C) second copepodid, dorsal.

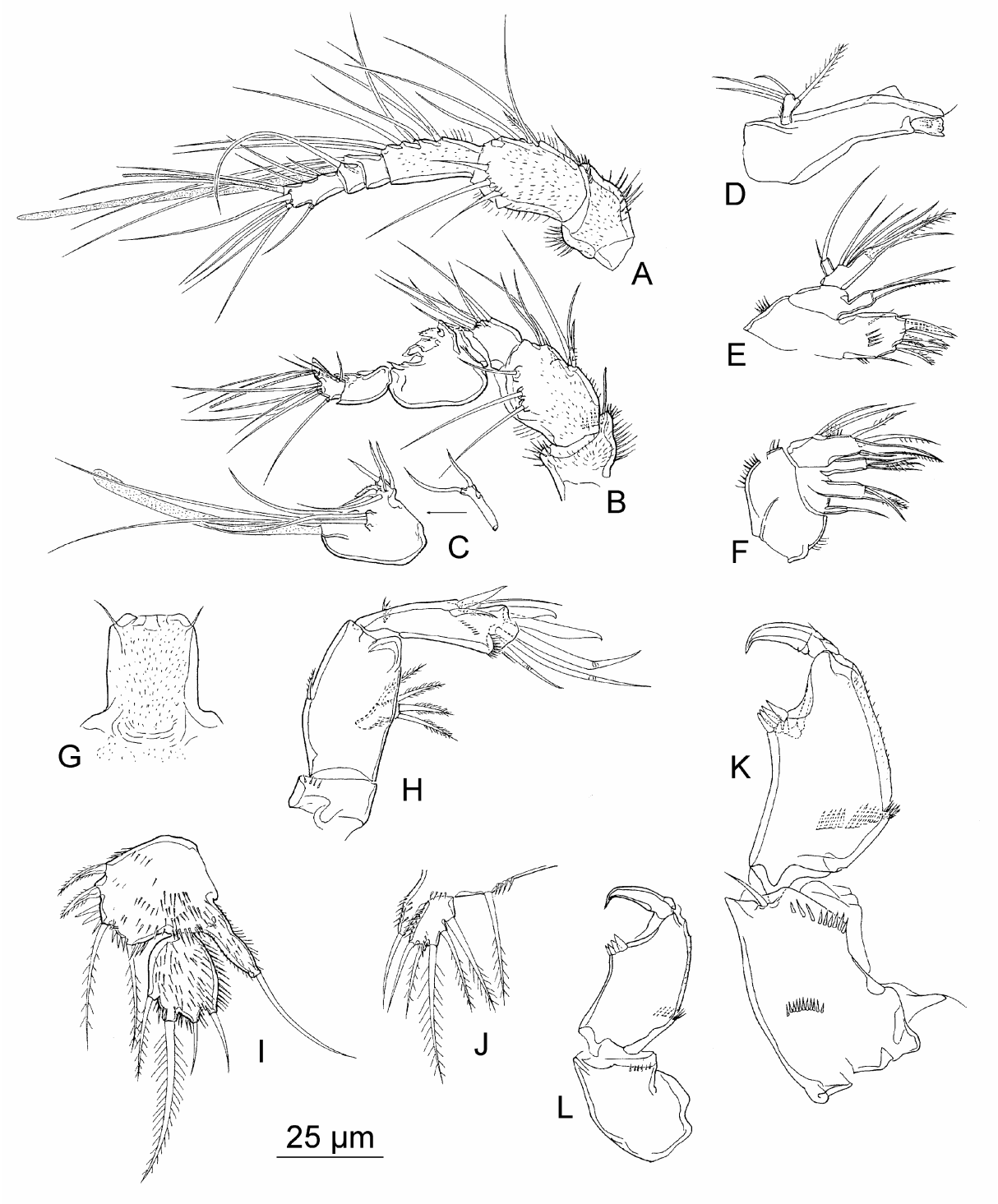

Figure 2. *Paralaophonte harpagone* sp. n. (A) female antennule, dorsal; (B) left male antennule (armature of segments IV and V omitted), dorsal; (C) right male antennule (segment IV and V), ventral; (D) female mandible; (E) female maxillule; (F) female maxilla; (G) female rostrum, dorsal; (H) female antenna; (I) female P5, anterior; (J) male P5, anterior; (K) female maxilliped; (L) second copepodid maxilliped.

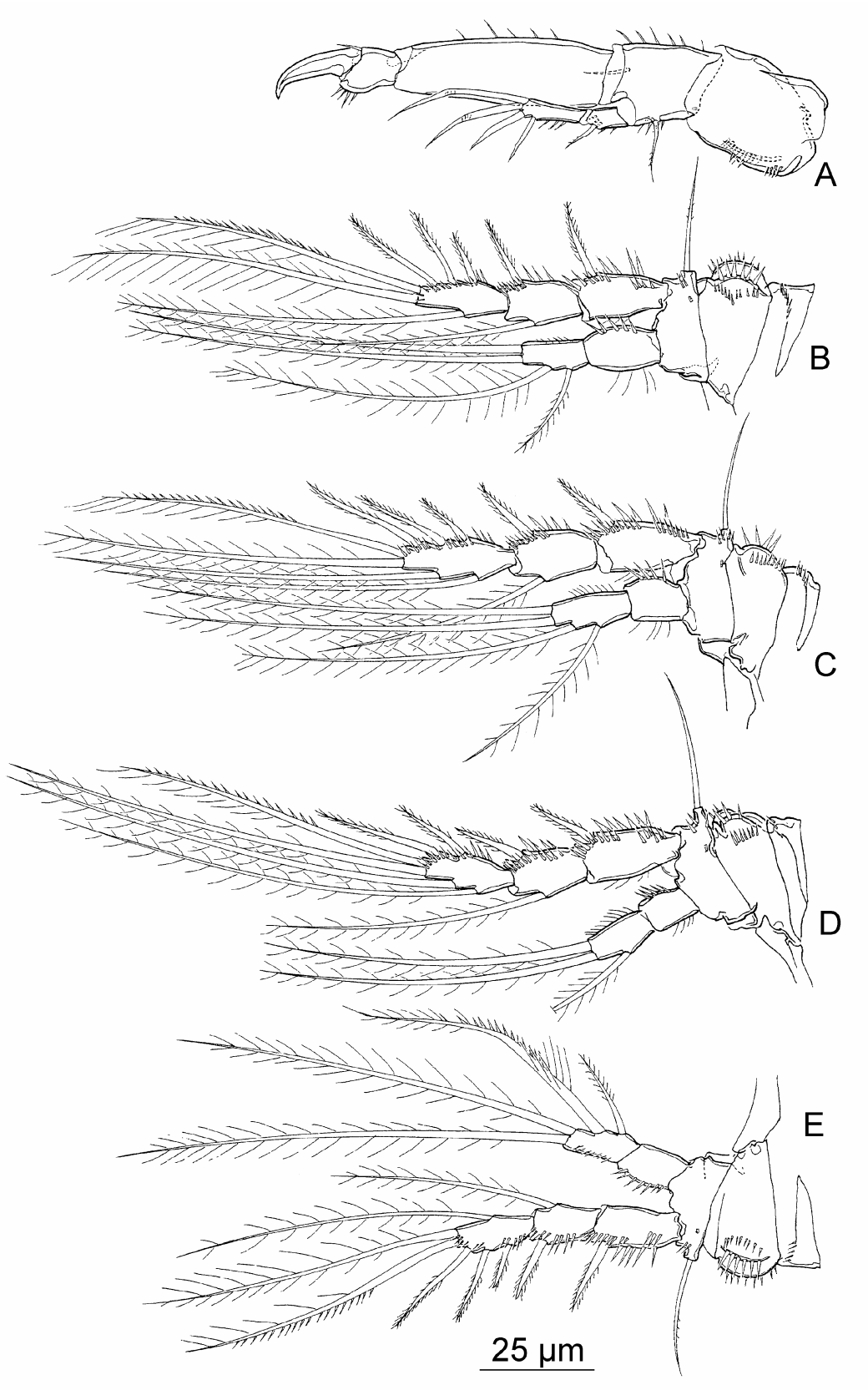

Figure 3. *Paralaophonte harpagone* sp. n. (A) female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) male P2, anterior.

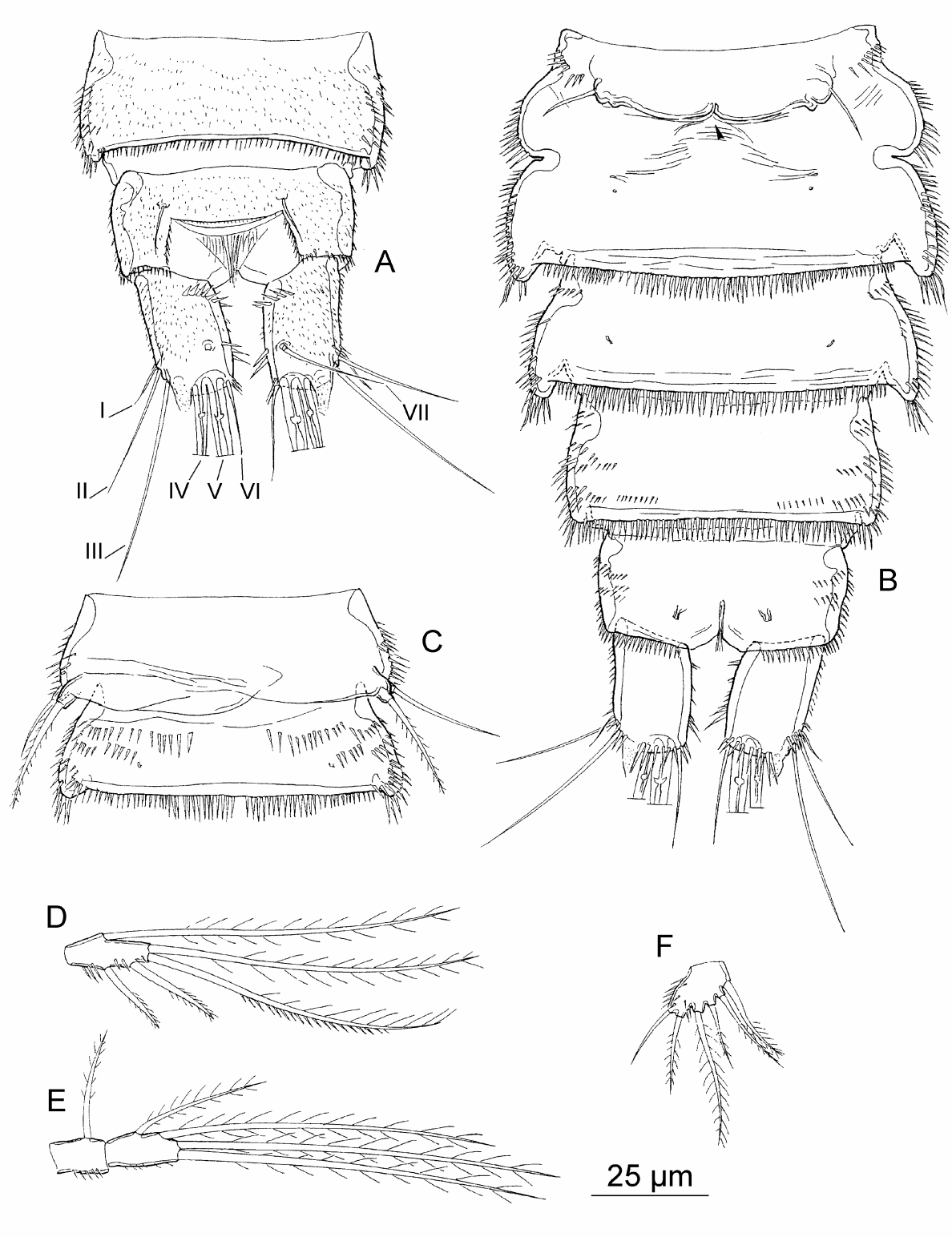

Figure 4. *Paralaophonte harpagone* sp. n. (A) female anal somite and caudal rami, dorsal; (B) female urosome (copulatory pore arrowed), ventral; (C) male second and third urosomite, ventral; (D) aberrant male P2 exp-3 (paratype), anterior; (E) aberrant male P3 enp (paratype), anterior; (F) aberrant male P5 exp (paratype), anterior.

6.5. DISCUSSION

Paralaophonte harpagone sp. n. occupies a very distinct position in the genus *Paralaophonte* Lang, 1944 because of the absence of any trace of sexual dimorphism in the endopodite of P3 and the exopodites of P2 to P4. However, the new species is a true representative of the genus *Paralaophonte* by the typical sexually dimorph P2 endopodite which is the major diagnostic feature of the genus. Nearly all members of *Paralaophonte* furthermore have a distinct sexually dimorph three-segmented P3 endopodite bearing an outer apophysis on the second segment. As discussed in Wells *et al.* (1982), four species have an only slightly modified male P3 endopod i. e. never three-segmented (*Paralaophonte perplexa* (T. Scott, 1898), *Paralaophonte quaterspinata* (Brian, 1917), *Paralaophonte innae* Chislenko, 1977 and *Paralaophonte aenigmaticum* Wells, Hicks & Coull, 1982; *Paralaophonte subterranea* Lang, 1965 was allocated to *Loureirophonte* Jakobi, 1953 in Fiers (1993)). In most species of *Paralaophonte*, the males have a distinctly modified, strongly built P3 exopod, whereas the exopods of P2 and P4 show little or no modification. Only in a few species the exopod of P3 is little or not modified compared to the female (*Paralaophonte macera* (Sars, 1908) and *Paralaophonte spitzbergensis* Mielke, 1974 with only stronger outer spines, *Paralaophonte innae* with exopods as in female). Another new species of *Paralaophonte*, which is currently under study, shows the typical sexually dimorph endopodites of P2 and P3, but lacks sexual dimorphism in the exopodites.

Mielke (1981) mentioned the several reduction tendencies in *Paralaophonte*, above all regarding the number of segments of the antennule, the number of exopodal segments of P1 and the chaetotaxy of the swimming legs. The present new species clearly exhibits these tendencies, in having only six antennular segments and two exopodal segments in P1. The chaetotaxy is highly reduced, without an outer seta on the endopodites of P3 and P4, enp-2 of P3 bears only two inner setae and exp-3 of P4 bears only two outer spines. *Paralaophonte quaterspinata* and *Paralaophonte innae* also lack an outer seta on enp-2 of P3 but still have the outer seta on enp-2 of P4. *Paralaophonte aenigmaticum* lacks the outer seta on the endopodites of both P3 and P4, but bears three inner setae on enp-2 of P3. *Paralaophonte aenigmaticum* and *Paralaophonte panamensis* Mielke, 1982 are the sole two species of *Paralaophonte*, apart from *Paralaophonte harpagone* sp. n., with only two outer spines on exp-3 of P4.

Paralaophonte Lang, 1944 is a large genus currently containing 33 species (including that described in this paper) (Lang, 1948; Bodin, 1997). The majority is benthic and freeliving but 3 species are true associates of the common spider crab *Maja squinado* (Herbst, 1788), namely *Paralaophonte royi* (Jakubisiak, 1932), *P. majae* Petkovski, 1964 and *P. ormieresi* Raibaut, 1968. However, none of them displays particular adaptations of body and appendages (personal observation of additional material of *P. royi*; Petkovski, 1964; Raibaut, 1968). Within the genus, *Paralaophonte harpagone* sp. n. has a unique chaetotaxy but the most distinguishing feature is the shape and position of the maxilliped, formerly unseen in *Paralaophonte*. The shape and particularly the robustness of the maxilliped is alike the strongly developed maxilliped of the genus

Namakosiramia Ho & Perkins, 1977 (Fig. 3F in Huys, 1988a; Fig. 2F in Kim, 1991). The latter consists of a robust syncoxa and basis, and a strong hook-like endopodite. The maxillipedal endopodite of *P. harpagone* sp. n. however is distinctly shorter. In both *Paralaophonte harpagone* sp. n. and *Namakosiramia* the maxillipeds are inserted near the lateral sides of the body and consequently are held almost entirely next to the body. However, the armature of the segments is different. While in *Namakosiramia* the syncoxa is asetose and the endopod bears two minute setae; in *Paralaophonte harpagone* sp. n. syncoxa and endopod each bear one seta (the endopodal one being minute). Originally, *Namakosiramia californiensis* Ho & Perkins, 1977 was placed in a new Cyclopoida family. Ho (1986) concluded it should have been placed in the Harpacticoida because of certain non-cyclopoid features. Huys (1988a) redescribed the species and effectively allocated it to the Laophontidae. In 1991, Kim described a second species, *Namakosiramia koreensis*, based on specimens of both sexes. Still, the systematic position within the family remains unclear, due to the extremely specialised body shape, the far-reaching reduction of buccal and locomotory appendages and the absence of sexually dimorph structures of the legs.

Namakosiramia californiensis exists as an ectoparasite on the holothurian *Stichopus parvimensis* (collected off Palos Verdes, California) (Ho & Perkins, 1977), while *Namakosiramia koreensis* was collected from the body surface of two species of holothurians from Korean waters (Kim, 1991). The maxilliped, P1 and P2 are powerful anchoring appendages to adhere to the host. All other postantennal appendages are strongly reduced in size and structure (Ho & Perkins, 1977; Huys, 1988a).

Among the other Laophontidae, a maxilliped of comparable robustness and position is not encountered, except in the newly described species. Based solely on the resemblance of this homologous structure (i.e. the maxilliped), it is hazardous to claim that *Namakosiramia* Ho & Perkins, 1977 belongs to the lineage *Paralaophonte* Lang, 1944 – *Loureirophonte* Jakobi, 1953. *Namakosiramia* is a valuable and distinctly defined genus with unique characteristics (e.g. absence of a process on segment 2 of A1, P2 stout and prehensile with exopodite forming a hook-like segment, P3-P5 vestigial). Furthermore, features which may clarify the relationship with *Paralaophonte*, i.e. the sexual dimorphism in the legs, are absent in the strongly reduced legs of *Namakosiramia*.

In the two samples containing *Paralaophonte harpagone* sp. n. no specimens were found attached to a possible invertebrate host (the 1 mm fraction contained mostly tanaidaceans and some small polychaetes, cumaceans and amphipods). Thusfar, we can only speculate whether the robust maxilliped may permit the species to exist as an associate of another invertebrate.

6.6. ACKNOWLEDGEMENTS

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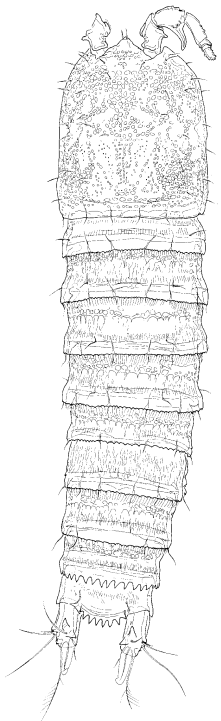
CHAPTER 7

Spiniferaphonte, a new genus of Laophontidae (Copepoda, Harpacticoida), with notes on the occurrence of processes on the caudal rami



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7.1. ABSTRACT

A new genus and species of Laophontidae, *Spiniferaphonte ornata* gen. n. sp. n., is described from the coast of Kenya. The new genus is closely related to *Laophontina* and *Wellsiphontina* as shown by the following synapomorphies: a denticulate operculum, a sexually dimorphic P4 exopod (reduced chaetotaxy of the ultimate segment in the male), and the absence of sexual dimorphism in the P2 and P3 endopods. The two-segmented exopod of P1 and the presence of a seta on the endopodal part of the male P5 are less derived, indicating that the new genus represents a separate lineage within this group. The proposal of the new genus *Spiniferaphonte* is supported by the following autapomorphies: three smooth setae on the female P5 exopod and a robust, dorsally bent, and strongly sclerotised caudal seta V. Within the Laophontidae, it is striking that the presence of distinct, thorn-like processes on the caudal rami is limited to interstitial genera. Distinct processes on the proximal segments of the antennule and a proximally thickened caudal seta V also appear to be associated with this interstitiality. These structures may play a role in the movement and the anchoring of the animals in their interstitial habitat.

Keywords: Harpacticoida, Laophontidae, *Spiniferaphonte* gen. n., caudal rami, interstitial

7.2. INTRODUCTION

As part of an extensive study of the copepod communities associated with the coral degradation zone, numerous qualitative samples of dead coral fragments, coral gravel, and coral sand were collected along the Kenyan coast. In terms of number of species, the family Laophontidae T. Scott, 1905 appears to be an important component of the copepod fauna associated with these substrates. Cottarelli & Puccetti (1988) also found this family to be a characteristic component of the interstitial fauna of coral beaches. It is noteworthy that 28 of the 44 species of Laophontidae until now determined from this study are new to science, including four species that have already been described[1] (Gheerardyn *et al.*, 2006a; Gheerardyn *et al.*, 2006c). Only 13 of the new species can be assigned unequivocally to existing genera, a fact that further highlights the high diversity of Laophontidae in this particular habitat. Another factor in the high proportion of taxonomic novelties is the hitherto limited number of species-level harpacticoid copepod studies in the western Indian Ocean: e.g., Madagascar (Chappuis, 1954), Réunion (Bozic, 1969), Seychelles (Wells & McKenzie, 1973), Mozambique (Wells, 1967), and Kenya (Fiers & De Troch, 2000; De Troch, 2001).

In a previous paper (Gheerardyn *et al.*, 2006a) a new genus of Laophontidae, *Peltidiphonte* Gheerardyn & Fiers, 2006, was established, containing three of the new Kenyan species. The most remarkable feature of this genus is the extremely depressed body shape, which was assumed to be an adaptation to live as epifauna on the surface of dead coral substrates.

[1] At the time of publication.

Specimens of the present new genus were collected from coarse coral gravel and clearly show adaptations for living in interstitial spaces, including a cylindrical body shape and reduced segmentation and setation of swimming legs P2 to P4. Dead coral substrates seem to provide a variety of habitats that are exploited by different Laophontidae with specialised morphologies. It is clear that the difficulties in unraveling the relationships within this family are mainly a consequence of a high degree of morphological plasticity.

7.3. MATERIAL AND METHODS

Meiofauna samples were collected from dead coral fragments along the Kenyan coast. Samples from coral gravel were obtained by decanting the coral gravel with filtered seawater (ten times) through a 32 μm sieve. Shortly after collecting, a buffered formaldehyde solution was added to a final concentration of 4%. In the laboratory, samples were centrifuged three times with Ludox HS40 (specific density 1.18) and finally stained with Rose Bengal. Harpacticoid copepods were sorted out and counted using a Wild M5 binocular microscope and were stored in 75% ethanol.

Observations and drawings were made from whole and dissected specimens mounted in glycerine, using a light microscope (Leica DM LS) equipped with a drawing tube. Preparations were sealed with insulating varnish. In toto specimens were stored in 75% ethanol. Type specimens are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, labelled COP). Scale bars in figures are indicated in μm.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth swimming legs; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of an exopod (endopod).

7.4. SYSTEMATICS

Family **Laophontidae T. Scott, 1905**
Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**
Genus ***Spiniferaphonte* Gheerardyn & Fiers gen. n.**

Diagnosis

Body cylindrical. Caudal rami bearing large, hook-like process anteriorly to seta VII, distinct process medially of seta VII, and several distinct processes along outer distal corner; seta V robust, dorsally bent, and strongly sclerotised. Genital field with 1 seta each on P6 vestiges and copulatory pore situated distinctly posteriad the transverse ridge. Antennule 6-segmented; segment 1 with blunt process proximally on dorsal surface, bump along inner margin, and process along outer margin. Segment 2 with large, posteriorly directed hook along outer margin. Antennary exopod bearing 4 sub-equal pinnate setae, lateral one being less densely pinnate. Exopod P1 2-segmented; exopod P2 1-segmented; exopods of P3 and P4 3-segmented.

Endopods of P2 to P4 each represented as single seta. Female P5 with 4 setae on baseoendopod; exopod with 5 setae, 3 of them smooth. Male P5 baseoendopod rudimentary with 1 seta on endopodal part; exopod with 3 setae.

Type species – *Spiniferaphonte ornata* Gheerardyn & Fiers, new species, monotypy.

Etymology – The generic name is derived from the Latin spina (meaning thorn), the Greek ferein (meaning to bear), and the suffix –phonte (gender feminine); and refers to the caudal rami bearing numerous thorn-like processes.

The above diagnosis coincides with that of the only known and type species of the genus, and must, therefore, be considered tentative.

***Spiniferaphonte ornata* Gheerardyn & Fiers gen. n., sp. n.** (Figures 1-5)

Type locality – Western Indian Ocean, Kenyan coast, Msambweni (4° 28' S, 39° 29' E), coarse coral gravel, water depth 2--3 m.

Material – From type locality: holotype ♀ dissected on 3 slides (COP4723a-c); allotype ♂ preserved in 70% alcohol (COP4724); paratypes, 2 ♀♀ preserved in 70% alcohol (COP4725); all collected 20 February 2002 by M. Raes.

Etymology – The specific name *ornata* (Latin, meaning ornamented) refers to the highly ornamented dorsal body surface.

Description of female

Total body length 564--610 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 135 μm.

Rostrum (Fig. 2A) large and prominent, broadly triangular, continuous with cephalothorax, with pair of sensilla anteriorly, dorsal surface pitted.

Habitus (Fig. 1A, B). Body cylindrical. Cephalothorax with parallel margins. Free prosomites as wide as cephalothorax. Urosome scarcely tapering posteriorly. Second and third urosomites fused to form genital double-somite but with transverse ridge dorsally and laterally indicating original segmentation; fully fused ventrally.

Integument of cephalothorax pitted but with symmetrical pattern of smooth areas; regularly ornamented with small sensilla. Surface of pleurotergites heavily ornamented, with pits in anterior half of each and fine striae in posterior half, except for surface of third urosomite completely striated. Dorsal surface of anal somite with few striae. Posterodorsal margin of cephalothorax smooth, those of free prosomites and following urosomites serrate, and that of penultimate somite strongly incised, forming large, tooth-like processes. Posterodorsal margins of cephalothorax and free somites (except penultimate urosomite) bearing several small sensilla; free prosomites and first urosomite additionally bearing 1 pair of sensilla dorsally. Posterodorsal margins of free prosomites and first, third, and fourth urosomites clothed with slender hairs.

Anal operculum distinctly backwardly produced, crescentic, flanked by 2 sensilla, and with strongly incised margin forming large, tooth-like processes.

Ventral surface (Fig. 5A) of genital double-somite heavily ornamented with pattern of striae. Lateral edges of genital double-somite and following urosomite with large, posteriorly directed, triangular processes. Ventral surface of fourth and fifth urosomite with rows of striae followed posteriad by row of short, slender spinules. Ventral surface of anal somite densely ornamented with symmetrical pattern of striae, that of fifth urosomite with short row of long, slender spinules laterally. Posteroventral margins of genital double-somite and following urosomites each bearing row of slender spinules.

Caudal rami (Fig. 5A, C, D) twice as long as wide; bearing conspicuous processes on dorsal surface and along inner and outer distal corners: viz., large, hook-like process anteriorly to seta VII, distinct process medially from seta VII, small process on outer distal corner of ramus, and 3 processes near implantations of setae I, II, and III. Dorsal surface of rami somewhat flattened with striae. Outer margin and distal ventral surface furnished with small spinules. Long, slender spinules present ventrally, with striae medial to them. Seta I, II, and III inserted in distal fourth of outer margin; seta I rudimentary. Seta IV and V not fused; seta IV pinnate; seta V robust, dorsally bent, strongly sclerotised. Seta VI short and slender; seta VII inserted in distal fourth of ramus.

Antennule (Fig. 2A) 6-segmented; majority of setae long and slender; segments 1-4 striated dorsally, smooth ventrally; segments 5 and 6 smooth. Segment 1 with blunt process proximally on dorsal surface, bump furnished with small spinules along inner margin, and sharp, thorn-like process along outer margin. Segment 2 with large, posteriorly directed hook along outer margin. Armature formula: 1-[1], 2-[7 + 1 pinnate], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[9 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 2 setae.

Antenna (Fig. 2B). Coxa bearing 2 rows of spinules. Allobasis with short, unipinnate abexopodal seta inserted in distal third. Exp unisegmented and small, bearing 4 sub-equal bipinnate setae with most lateral one being less densely pinnate. Enp with few spinules, 2 sub-apical frills, and following armature: subapically, 2 unipinnate, long spines and 1 rudimentary seta, and apically, 2 robust spines (one of them armed), 3 geniculate setae (one being pinnate), and 1 small, slender seta.

Mandible (Fig. 2C) with well developed, strongly sclerotised gnathobase bearing several blunt teeth and 1 unipinnate seta. Spinule row near insertion of palp. Palp uniramous, exopod represented as short seta, endopod with faint suture and bearing 3 setae. Basal armature represented by plumose seta.

Maxillule (Fig. 2D). Praecoxal arthrite well developed; bearing row of long spinules on posterior surface; medial margin furnished with 8 spines/setae; 1 seta on anterior surface. Coxal endite with 1 pinnate seta and 1 naked seta. Basal endite with 3 setae. Endopod obsolete, represented by 1 pinnate and 2 naked setae. Exopod 1-segmented with 2 apical setae.

Maxilla (Fig. 2E). Syncoxa with row of long spinules along outer edge, 2 short spinule rows on posterior surface, and row of short spinules along inner margin; with 3 endites. Praecoxal

endite small, with 1 seta. Proximal coxal endite with strong pinnate spine and 2 slender setae. Distal coxal endite with strong pinnate spine, pinnate seta, and naked seta. Allobasis drawn out into strong, slightly curved, armed claw bearing 2 setae. Endopod obsolete, represented by 3 naked setae.

Maxilliped (Fig. 3E). Syncoxa with a spinule row and 1 pinnate seta, latter inserted distally. Endopod long and slender, slightly curved, armed with short, naked seta at base.

P1 (Fig. 3A). Coxa cylindrical with 2 rows of short spinules along outer margin and slender hairs along inner margin; anterior surface with striae. Basis with 1 seta on outer margin, medial seta arising on anterior surface, short spinule row near outer seta, and tube pore near articulation with coxa. Exp-1 furnished with spinules and unipinnate outer seta; exp-2 with 3 naked outer setae and 2 geniculate apical setae. Enp-1 without spinules; enp-2 with armed claw, minute, naked accessory seta, and few spinules. Enp-1 2.5 times as long as exopod.

P2-P4 (Fig. 3B, C, D). Prae-coxae small and triangular. Coxae completely fused to intercoxal sclerites, these being striated. Short spinule row along outer distal margin of coxae. Bases with tube pore on anterior surface and a rather short, pinnate (P2) or long, naked (P3, P4) basal seta arising from distinct lateral setophore, latter bulbous in P2. Each endopod of P2-P4 represented as a single strong, plumose seta. Exopods of P2-P4 small, of compact appearance, that of P2 1-segmented, those of P3 and P4 3-segmented. Setal formula in Table 1. Segments with patterns of spinules as figured.

P5 (Fig. 3F) with separate exopod and baseoendopod, both covered anteriorly with fine striae; margins bearing long, slender spinules or stout, short spinules, and some spinule rows on anterior surface of baseoendopod. Basal seta arising from long setophore. Endopodal lobe extending almost to middle of exopod and bearing 4 plumose setae. Exopod rounded, somewhat longer than wide with 2 bumps along inner margin, bearing 2 plumose (i.e. innermost and second outermost) and 3 slender, smooth setae, all closely set in distal region.

P6 vestiges (Fig. 5A) each bearing 1 naked seta, with 2 small processes set medially from it. Copulatory pore situated distinctly posteriad the transverse ridge connecting the pair of P6.

Description of male

Total body length 562 μm (measured from anterior margin of rostrum to posterior margin of caudal rami). Greatest width measured at posterior margin of cephalothorax: 124 μm.

Habitus as in female, except for the fully separated second and third urosomites and fewer posteriorly directed triangular processes along lateral edges of third and fourth urosomites (Fig. 5B). Ventral surface of second urosomite heavily ornamented with pattern of striae in anterior half; that of third and fourth urosomites with a row of long, slender spinules laterally.

Antennule (Fig. 4C, 4D) 8-segmented; sub-chirocer. Segments 1 and 2 as in female. Armature formula: 1-[1], 2-[8 + 1 pinnate], 3-[7], 4-[2], 5-[8 + 1 pinnate + (1 + ae)], 6-[0], 7-[0 (?)], 8-[10(?)].

Antenna, mouthparts, and P1-P3 as in female.

P4 (Fig. 4A). Seta representing endopod shorter than in female. Exp-2 and exp-3 with 3 and 2 processes, respectively, along outer margin. Exp-3 lacking inner seta.

P5 (Fig. 4B). Endopodal lobe of baseoendopod obsolete; bearing 1 plumose seta with tube pore medially next to it. Basal part with outer naked seta arising from setophore (latter bearing a tube-pore proximally). Exopod convex along inner margin; almost twice as long as maximum width; bearing 3 setae closely set apically, outer seta long and 2 inner setae short and more slender; inner and outer margins set with spinules.

P6 vestiges (Fig. 5B) asymmetrical. One vestige functional, other fused to somite. Both produced into slender, cylindrical process bearing 1 inner pinnate seta and 1 outer smooth seta.

Variability – One female paratype has a left P2 exopod bearing only 3 setae; the other female paratype has a left P3 exopod with an inner seta on the third segment.

	Exopod	Endopod*
P2	022	1
P3	0.0.021	1
P4	0.0.121 [0.0.021 in ♂]	1

Table 1. *Spiniferaphonte ornata* gen. n., sp. n. Swimming leg setal formula.
(* The endopod of P2-P4 is only represented by a seta.)

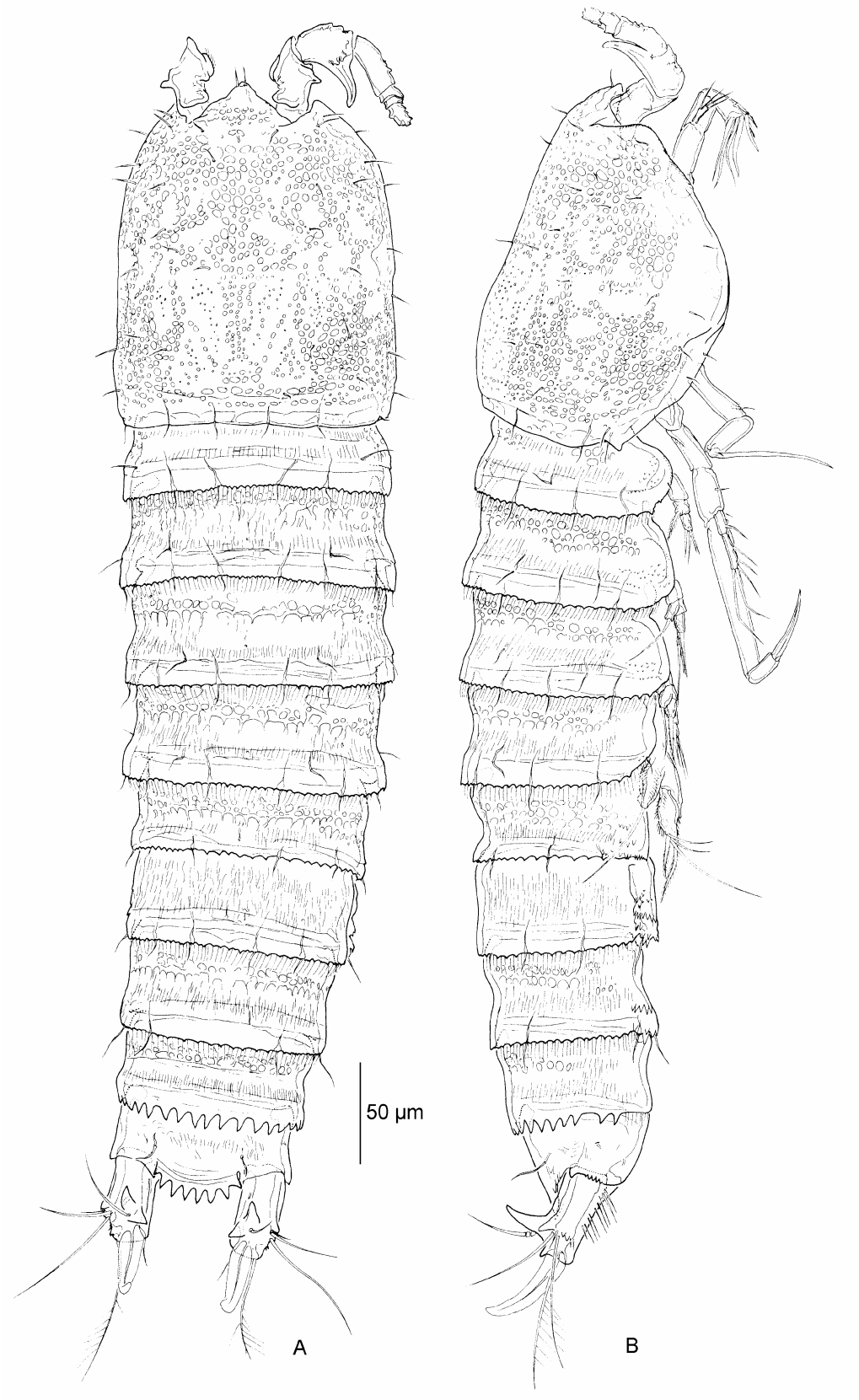

Figure 1. *Spiniferaphonte ornata* gen. n., sp. n., holotype. (A) female habitus, dorsal; (B) female habitus (mandible, maxillule, and maxilla omitted), lateral.

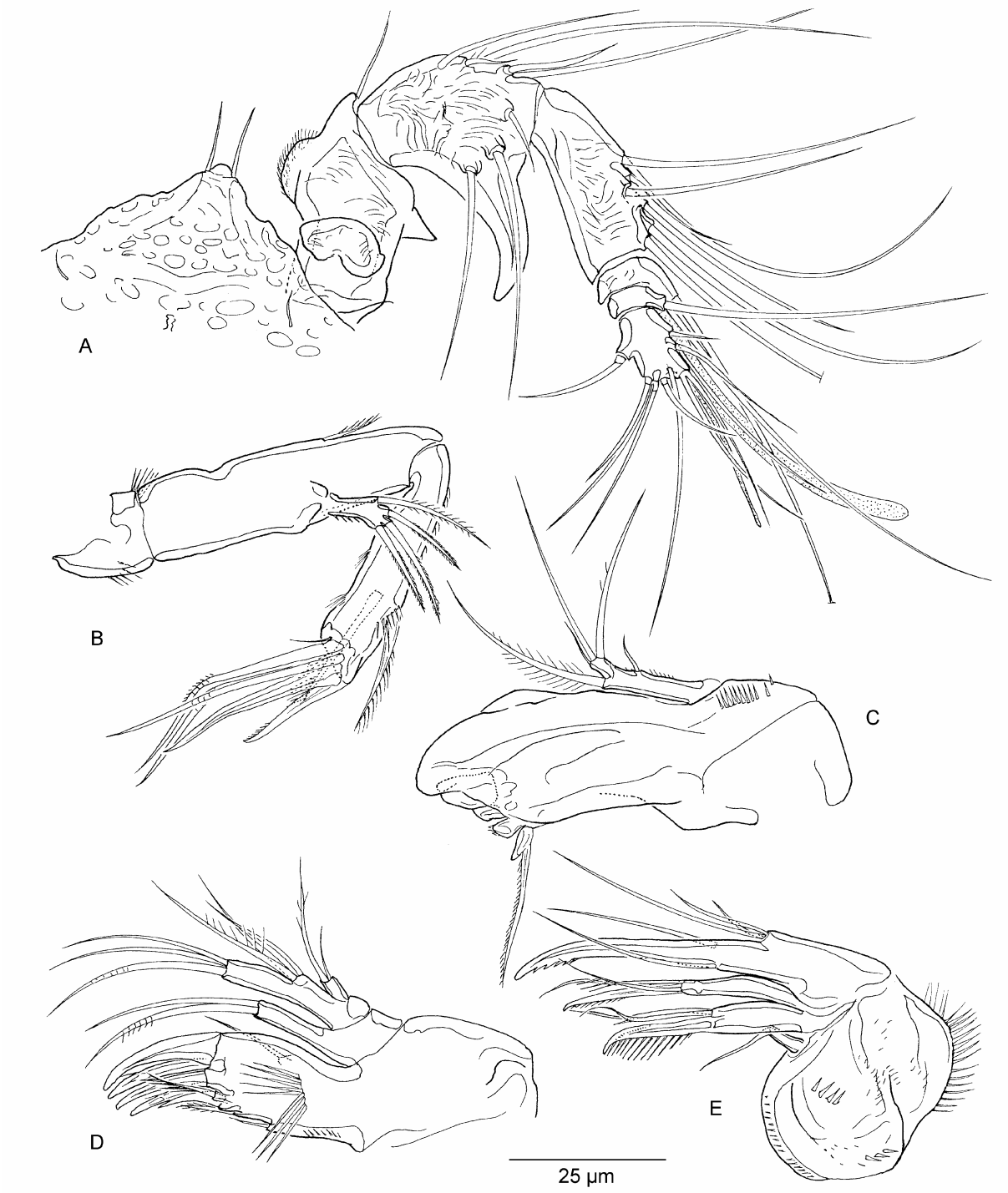

Figure 2. *Spiniferaphonte ornata* gen. n., sp. n., holotype. (A) female antennule and rostrum, dorsal; (B) female antenna; (C) female mandible; (D) female maxillule; (E) female maxilla.

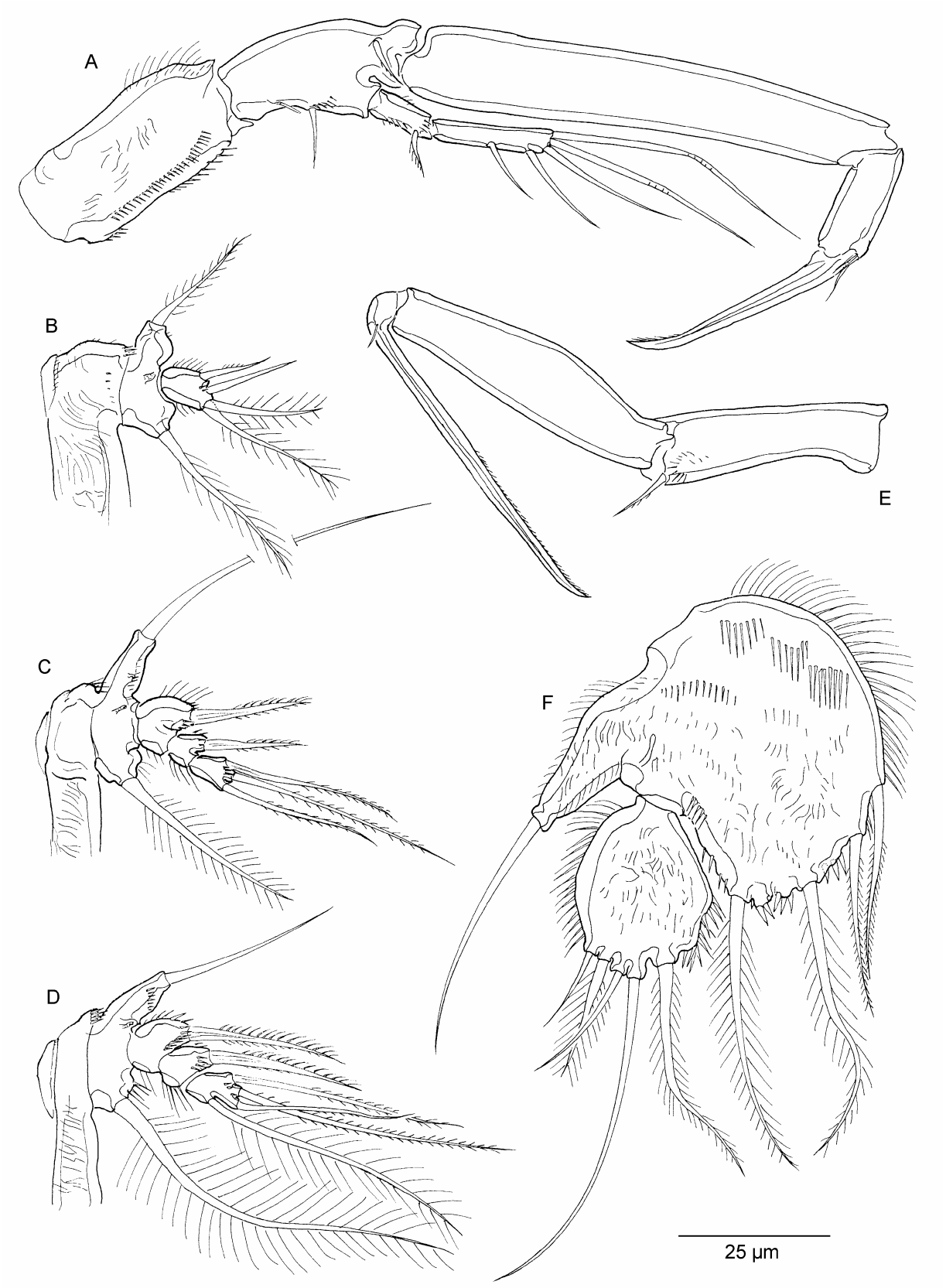

Figure 3. *Spiniferaphonte ornata* gen. n., sp. n.,holotype. (A) female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) female maxilliped; (F) female P5, anterior.

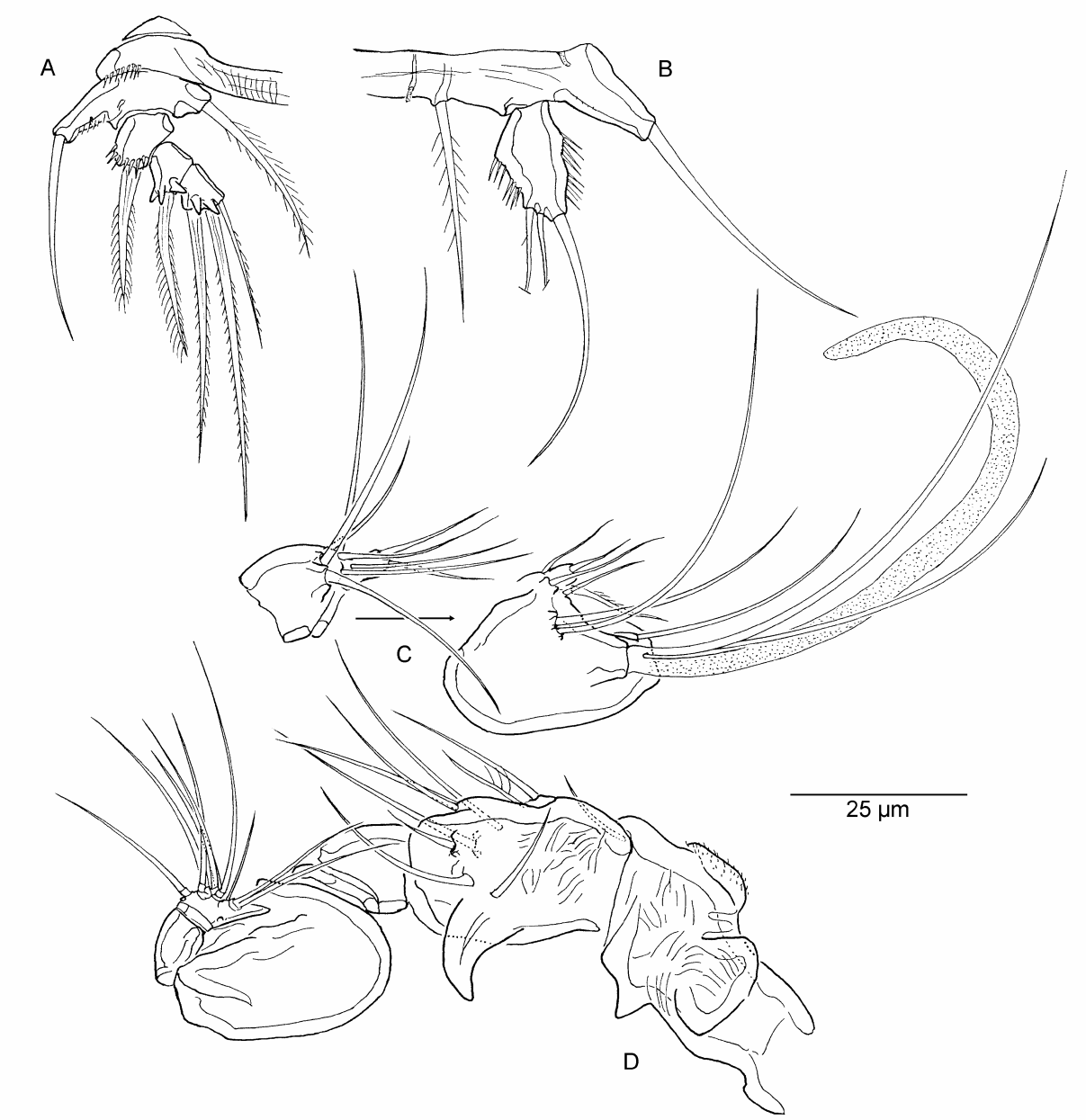

Figure 4. *Spiniferaphonte ornata*, gen. n., sp. n., allotype. (A) male P4, anterior; (B) male P5, anterior; (C) male antennule (segments 3 to 5), ventral; (D) male antennule (armature of segments 3 to 5 omitted), dorsal.

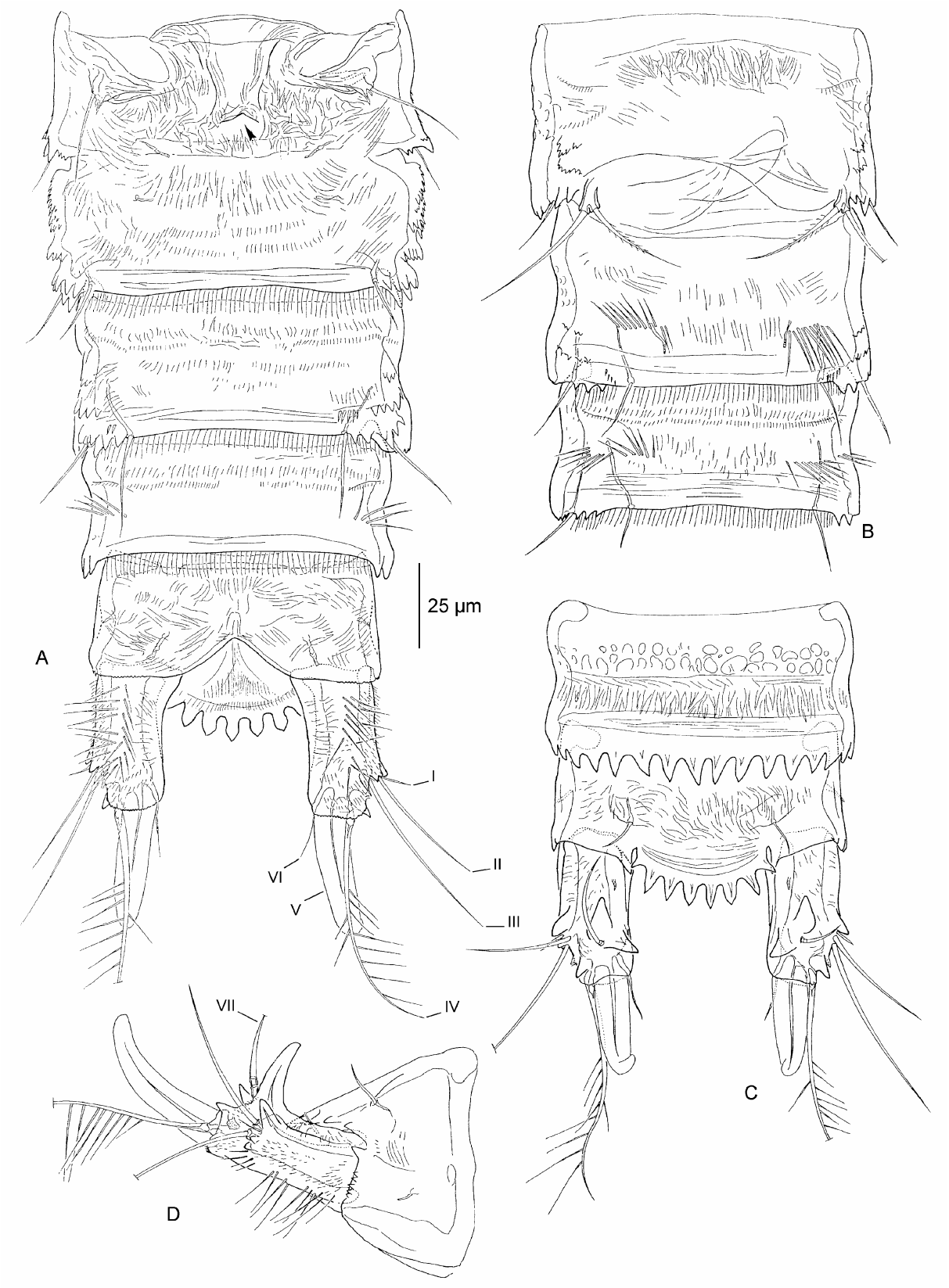

Figure 5. *Spiniferaphonte ornata* gen. n., sp. n., holotype and allotype. (A) female urosome (copulatory pore arrowed), ventral; (B) male second to fourth urosomite, ventral; (C) female anal somite and caudal rami, dorsal; (D) female anal somite and caudal ramus, lateral.

7.5. DISCUSSION

In the family Laophontidae, several genera (such as *Arenolaophonte* Lang, 1965, *Galapalaophonte* Mielke, 1981 *sensu* Fiers (1991b), *Indolaophonte* Cottarelli, Saporito & Puccetti, 1985, *Laophontina* Norman and T. Scott, 1905 *sensu* Fiers (1991b), and *Mexicolaophonte* Cottarelli, 1977) have similar adaptations to an interstitial life style, namely a cylindrical body shape and a reduced segmentation and/or setation of the swimming legs P2-P4. Even when three segments remain in a particular ramus, generally they are of small size or of peculiar shape (Wells & Rao, 1987). These similar adaptations, also present in *Spiniferaphonte* gen. n., are undoubtedly the result of convergent evolution in as much as certain of these genera belong to different lineages. Vermiform genera (e.g., *Afrolaophonte* Chappuis, 1960 and *Klieonychocamptoides* Noodt, 1958) are characterised by reduction of the posteriorly directed lateral processes of both somites of the genital double-somite (Huys, 1990). Together with the reduction of the swimming legs, these also are adaptations to an interstitial life style.

Fiers (1991) thoroughly revised the genus *Laophontina*, as it was then known, and divided it into four different genera: *Amerolaophontina* Fiers, 1991, *Galapalaophonte*, *Laophontina*, and *Wellsiphontina* Fiers, 1991. All of these genera show the typical modifications for an interstitial life style. Distinction between the different genera was mainly based on the genital field, sexual dimorphism of the swimming legs, integumental structures, ornamentation of the anal operculum, and P5 chaetotaxy. It was supposed that the *Galapalaophonte-Amerolaophontina* lineage branched off from a different stock than *Laophontina* and *Wellsiphontina*. *Galapalaophonte* is markedly characterised by peculiar, sexually dimorphic endopods of P2 and P3 and a median thorn on the anal operculum. The genus has an amphi-American distribution. Although *Amerolaophontina* lacks markedly sexually dimorphic endopods and has strongly reduced swimming legs, it is plausible to assume that it shares a common ancestor with *Galapalaophonte*. *Wellsiphontina* seems most closely related to *Laophontina*, as is shown by the denticulate operculum and the typically transformed male P4, both considered to be synapomorphic states. In both genera the male P4 is considerably smaller, bears much stronger exopodal spines, and has fewer elements on the ultimate segment than the female P4. While *Wellsiphontina* has a restricted distribution along East African shores, *Laophontina* occurs in the Mediterranean and the eastern Atlantic.

A single juvenile specimen from the Seychelles, classified as Laophontidae gen. spec. male copepodid V in Fiers (1991b), appears to be closely related to *Spiniferaphonte ornata*. Although this specimen is a copepodid, its features indicate a close affinity to the present new species. The processes on the first and second segment of the A1 are similarly positioned. The P1 exopod will probably be organised into a two-segmented one in the adult stage. The endopods of P2-P4 are each represented by a single seta, and the respective exopods will most likely be at least two-segmented (as indicated by the number of outer exopodal spines, by reference to the copepodid development of *Galapalaophonte biarticulata* Fiers, 1991 (see: fig. 21 Fiers, 1991b). There are distinct, thorn-like processes at similar positions on the caudal rami, a strongly sclerotised seta V

without a slender distal part, and long, slender spinules on the ventral surface of the caudal rami. Finally, the strong, tooth-like, mediodorsal processes on the anal somite most likely will form a strongly incised posterior rim of the adult penultimate somite. Fiers (1991b) already supposed this juvenile to be more closely related to *Wellsiphontina* than to the *Galapalaophonte-Amerolaophontina* lineage.

Although *Spiniferaphonte* shares certain characteristics with the *Galapalaophonte-Amerolaophontina* lineage (the pitted cephalothorax, P6 with one seta, copulatory pore posteriad the transverse ridge), it seems more plausible for *Spiniferaphonte* to have originated from the same stock as *Wellsiphontina* and *Laophontina*. This close relationship is supported by the following synapomorphies: a denticulate operculum, a sexually dimorphic P4 exopod (reduced chaetotaxy of the ultimate segment in the male), and the absence of sexual dimorphism in the P2 and P3 endopods. The proposal of the new genus *Spiniferaphonte*, for *S. ornata*, new species, is supported by the following autapomorphies: three smooth setae on the female P5 exopod and a robust, dorsally bent, and strongly sclerotised caudal seta V. In addition, the genus exhibits following less derived characteristics: the two-segmented P1 exopod and the presence of a seta on the endopodal part of the male P5, that indicate the new species represents a separate lineage and, therefore, it is assigned to a new genus.

Within the Laophontidae, the variety in shape of the caudal rami is relatively large, compared to other families (personal observation). Mostly, the rami are short (one to two times as long as wide) and cylindrical, but they can be up to eight times as long as wide (e.g., *Archilaophonte* Willen, 1995, *Echinolaophonte mirabilis* (Gurney, 1927), *Laophonte elongata* Boeck, 1872). Lamelliform caudal rami that are flattened, broad, and oval are typical for the genera *Asellopsis* Brady and Robertson, 1873 and *Tapholeon* Wells, 1967 and also occur in two species of *Paralaophonte* Lang, 1944 (viz., *P. asellopsiformis* Lang, 1965 and *P. aenigmaticum* Wells, Hicks & Coull, 1982) (Huys, 1990).

Certain genera bear one or more upwardly directed processes on the dorsal surface of the caudal rami (*Amerolaophontina*, *Galapalaophonte*, *Indolaophonte*, *Langia* Wells & Rao, 1987, *Laophontina*, *Mexicolaophonte*, *Pseudolaophonte* A. Scott, 1896, *Spiniferaphonte*, and *Wellsiphontina*) (Bodin, 1977; Cottarelli, 1977; Cottarelli, Saporito & Puccetti, 1986; Fiers, 1991b; Wells & Rao, 1987). At first sight, these genera appear to be related to each other on other grounds, such as similarities in A1, body shape, and reduction of the swimming legs. The position of the processes on the caudal rami can be taken as a criterion to define two groups among them. Lang (1948) already noted that the caudal rami offer useful systematic characters, and Huys (1988b) stressed the importance of their morphology in helping to reveal relationships among paramesochrid genera. In *Indolaophonte* and *Langia* a spinous process is developed and is derived from a posterior outgrowth of the posterolateral corner of each caudal ramus (see: fig. II,1 Cottarelli, Saporito & Puccetti, 1986; fig. 5C Mielke, 1997), while in the other genera a spinous process is developed medially of or anteriorly to seta VII (see: fig. 4 Bodin, 1977; fig. 2b Cottarelli, 1977; fig. 8b, 12a, 24a Fiers, 1991b). These differently positioned processes are considered here as different derived

conditions of the normal cylindrical caudal rami which do not bear any processes. As in all Copepoda, the cylindrical caudal rami are the most generalised form which is known as the ancestral one (Huys & Boxshall, 1991). Although the latter group of genera shares a derived characteristic (namely a similarly positioned novel structure), the exact relationships (apart from the above-mentioned affinities) between these genera remain difficult to assess.

The outer distal process on the caudal ramus is a distinct synapomorphy of *Indolaophonte* and *Langia* that demonstrates their shared and distinct path of descent. The close relationship between these two genera is furthermore shown by the similar A1, exopod of A2 (bearing 3 setae), and male and female P5. Detailed study (e.g., of body surface and mouthparts) of the two species of *Indolaophonte* should reveal whether *Langia maculata* Wells & Rao, 1987 can also be included in *Indolaophonte* with an accordingly adjusted generic diagnosis. Mielke (1997) provided a redescription of *L. maculata* but did not discuss this possible relationship. At present, the monospecific *Langia* is mainly distinguished from *Indolaophonte* because of the presence of a two-segmented P2 exopod and a three-segmented P3 exopod (versus one-segmented and two-segmented, respectively, in *Indolaophonte*).

In certain genera, one of the apical caudal setae is modified. In *Pseudolaophonte*, the terminal accessory seta (seta VI) is modified into a strong, dorsally bent spine that is equal in length to the caudal ramus itself (see: fig. 4 Bodin, 1977; Klie, 1950). It is not unlikely that this modified seta is a functional analogue of the dorsal process on the apical margin of each caudal ramus in *Indolaophonte* and *Langia*, both of which are interstitial genera. In the genera *Laophontina*, *Wellsiphontina*, *Amerolaophontina*, *Galapalaophonte*, *Mexicolaophonte*, and *Maiquilaophonte* Mielke, 1985, and in certain species of *Klieonychocamptoides*, the inner terminal seta (seta V) is thickened proximally, with a thorn-like process dorsally at a certain point, posteriorly from which it continues as a slender seta (see: fig. 2b Cottarelli, 1977; fig. 3c, 5c, 10b, 24a Fiers, 1991b; fig. 44 Mielke, 1981; fig. 49C Mielke, 1985). In *Spiniferaphonte*, caudal seta V is a strongly sclerotised, dorsally bent seta, apparently having lost the slender distal part.

It is striking that a modified seta V (which is present in both sexes) only occurs in interstitial species and is mostly associated with distinct processes on the caudal rami and/or the anal operculum. The members of these genera also bear strong, thorn-like processes on the proximal segments of the antennule (see: fig. 2a Cottarelli, 1977; fig. 2g, 6a, 11b, 23b Fiers, 1991b; fig. 42C Mielke, 1981; fig. 45C Mielke, 1985). Kunz (1974) described *Kliopsyllus furcavaricatus* (Kunz, 1974) from coral sand. This paramesochrid is characterised by the ability to spread its caudal rami. As a consequence, the dorsally bent, thorn-like processes on the anal somite, which serve as antagonistic structures, are flexed upwardly. Kunz (1974) presented two explanations for this spreading behaviour. The mechanism might be useful in moving through the interstitial habitat; it might also function in anchoring the animal between sand grains when interstitial water moves due to wave action. These explanations may well apply to the mentioned laophontids, in which the modified caudal seta and the strong, thorn-like processes on the antennules and caudal rami may play a role in the movement and anchoring of the animals in their interstitial habitat.

7.6. ACKNOWLEDGEMENTS

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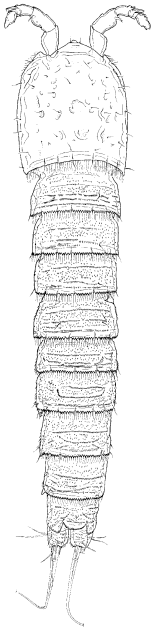
CHAPTER 8

Revision of the genus *Tapholeon* Wells, 1967 (Copepoda, Harpacticoida, Laophontidae)



Paper in press

Gheerardyn, H., Fiers, F., Vincx, M., De Troch, M.
Revision of the genus *Tapholeon* Wells, 1967 (Copepoda, Harpacticoida, Laophontidae).
Journal of Natural History.

8.1. ABSTRACT

To date, only two species are known in the laophontid genus *Tapholeon* Wells, 1967 (Copepoda, Harpacticoida). In the present contribution, a redescription of the type species *T. ornatus* Wells, 1967, based on the type material, is provided. Furthermore, two new species are described from the coast of Kenya, *T. inconspicuus* sp. nov. and *T. tenuis* sp. nov. Two species, formerly attributed to *Asellopsis* Brady & Robertson, 1873 (viz. *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), are allocated to *Tapholeon* based on the absence of sexual dimorphism in the swimming legs P2 to P4. The former of the two species is redescribed based on additional material from the Comoros. An updated generic diagnosis and a key to the six species of *Tapholeon* are included.

Keywords: Laophontidae, *Tapholeon*, redescription, new species

8.2. INTRODUCTION

The present paper is part of an extensive study of the copepod fauna associated with the coral degradation zone along the eastern coasts of Kenya and Zanzibar (Tanzania). In the lagoon, between the reef and the beach, different substrates, ranging from coral sand, fine coral gravel and coral rubble to large coral fragments, were sampled. To date, the qualitative samples from the Kenyan coast yielded 44 species of the family Laophontidae T. Scott, 1905, including 28 which are new to science (four species have been described so far[1] (Gheerardyn *et al.*, 2006a; Gheerardyn *et al.*, 2006c). Two new Kenyan species are described here and recognised within the genus *Tapholeon* Wells, 1967. Hitherto, this genus consisted of only two species, *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967, both described from Inhaca Island (Mozambique). Wells (1967) established this genus mainly based on the complete absence of sexual dimorphism in the swimming legs P2-P4. Here we provide a redescription of the type species *T. ornatus*, based on the re-examination of the type material. Furthermore, two species, formerly attributed to *Asellopsis* Brady & Robertson, 1873 (viz. *A. arenicola* Chappuis, 1954 and *A. chappuisius* Krishnaswamy, 1957), are allocated to *Tapholeon*. Based on additional material from the Comoros, the former of these two species is redescribed.

8.3. MATERIAL AND METHODS

Along the eastern coast of Kenya (2002), meiofauna samples were collected from various dead coral substrates (ranging from coral sand, fine coral gravel and coral rubble to large coral fragments). Prior to fixation, epifauna from coral fragments and coral rubble were rinsed off with filtered seawater over a 1 mm and a 32 μm sieve. Samples from coral gravel were obtained by decanting the coral gravel (ten times) over a 32 μm sieve. Buffered formaldehyde was added to a final concentration of 4%. In the laboratory, samples were centrifuged three times with Ludox HS40 (specific density 1.18) and finally stained with Rose Bengal.

[1] At the time of publication.

On Grande Comore (1981), several samples of sediments were collected following a slightly different procedure. To the sampled substrates, buffered formaldehyde was added immediately to a final concentration of 4%. In the laboratory, samples were rinsed with a jet of freshwater over a 5 mm and a 45 μm sieve, and centrifuged three times with Ludox HS40 (specific density 1.18).

Harpacticoid copepods were counted using a Wild M5 binocular, were sorted out and stored in 75% ethanol. Observations and drawings were made from whole and dissected specimens mounted in lactophenol, using a light microscope (Leica DM LS) equipped with a drawing tube. Preparations were sealed with insulating varnish. In toto specimens were stored in 75% ethanol. The type specimens of *Tapholeon inconspicuus* Gheerardyn and Fiers sp. nov. and *T. tenuis* Gheerardyn and Fiers sp. nov. are deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, labelled COP). Specimens of the type series of *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967 were loaned from the Natural History Museum, London. Scale bars in figures are indicated in μm.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus.

8.4. SYSTEMATICS

Family **Laophontidae T. Scott, 1905**

Subfamily **Laophontinae T. Scott, 1905 *sensu* Huys & Lee, 2000**

Genus ***Tapholeon* Wells, 1967**

Updated diagnosis

Laophontidae. Habitus slender and elongate, slightly depressed dorso-ventrally; with distinct convex curvature in lateral aspect; without demarcation between prosome and urosome. Cephalothorax slightly longer than wide, with parallel margins. Urosome only slightly tapering posteriorly. Anal operculum convex with serrate margin, not distinctly protruding. Caudal rami dorso-ventrally flattened. Dorsal surface depressed beyond implantation of seta VII. Seta IV and V rather short.

Sexual dimorphism in body size, antennule, P5, P6, genital segmentation and ornamentation of ventral surface of urosome.

Rostrum prominent, fused to cephalothorax. Female antennule five- or six-segmented. Male antennule sub-chirocer. Second segment (both sexes) bearing small blunt process and strong, armed spine along posterior margin. Ultimate segment of female antennule bearing (at least) two stout setae. Antenna with reduced abexopodal seta on allobasis. Antennary exopod well developed; bearing four setae (one of which dwarfed). Mandibular palp uniramous, bearing one, one, three setae, representing basis, exopod and endopod, respectively. Maxillule with two elements on coxal endite; basal endite with two setae and one curved spine; endopod represented by three setae; exopod with two setae. Maxillary syncoxa with three endites; praecoxal endite

small, with one seta; both coxal endites with three elements; allobasis drawn out into claw, with two accessory elements; endopod represented by two setae. Maxilliped subchelate; syncoxa with one seta; endopod clawshaped with one short seta at base. Exopod P1 one- or two-segmented. Swimming legs P2-P4 with two-segmented endopods and three-segmented exopods. Swimming leg setal formulae in Table 1. Without sexual dimorphism in P2-P4. P5 with separate exopod and baseoendopod. Female P5 with endopodal lobe reaching at least to middle of exopod, bearing one apical and three lateral setae; exopod ovate to rhomboid, bearing five setae. Male P5 baseoendopod obsolete, without endopodal seta; exopod small, bearing three or four setae. P6 vestiges bearing one seta in female; vestiges asymmetrical in male, with each outer distal corner produced into cylindrical process bearing two setae.

Type species – *Tapholeon ornatus* Wells, 1967

Other species – *T. arenicolus* (Chappuis, 1954) comb. nov.; *T. chappuisius* (Krishnaswamy, 1957) comb. nov.; *T. inconspicuus* Gheerardyn & Fiers sp. nov.; *T. tenuis* Gheerardyn & Fiers sp. nov.; *T. uniarticulatus* Wells, 1967

	P1	P2		P3		P4	
	exp	exp	enp	exp	enp	exp	enp
Tapholeon inconspicuus	1	0.1.123	0.120	0.1.223	0.221	0.1.223	0.121
Tapholeon tenuis	2	0.1.123	0.220	0.1.223	0.220	0.1.223	0.120
Tapholeon ornatus	2	0.1.123	0.120	0.1.223	0.220	0.0.223	0.120
Tapholeon arenicolus	2	0.1.123	0.020	0.1.223	0.120	0.0.223	0.120
Tapholeon uniarticulatus	1	0.1.122	0.120	0.1.222	0.121	0.1.222	0.121
Tapholeon chappuisius	2	0.1.122	0.020	0.1.222	0.020	0.1.222	0.020

Table 1. Species of *Tapholeon* Wells, 1967. Number of exopodal segments in P1 and swimming leg setal formulae of P2-P4.

***Tapholeon ornatus* Wells, 1967** (Figures 1-4)

Type locality – Mozambique, Inhaca Island: Ilha dos Portuguesos, Barriera Vermelha beach (clean sand) and Saco da Inhaca (detritus sand) (Wells 1967).

Type material – Type specimens are deposited in the British Museum of Natural History, London (Wells 1967).

Material examined – (a) Type material: one female holotype dissected on one slide (NHM 1967.8.4.106), one male paratype in one slide (NHM 1967.8.4.107), one female paratype in one slide (NHM 1967.8.4.108), one male and three female paratypes in 70% alcohol (NHM 1967.8.4.109), one female paratype dissected on five slides (NHM 2006.1492), one female paratype dissected on four slides (NHM 2006.1493), and one male paratype in one slide (NHM 2006.1494); all from the type locality.

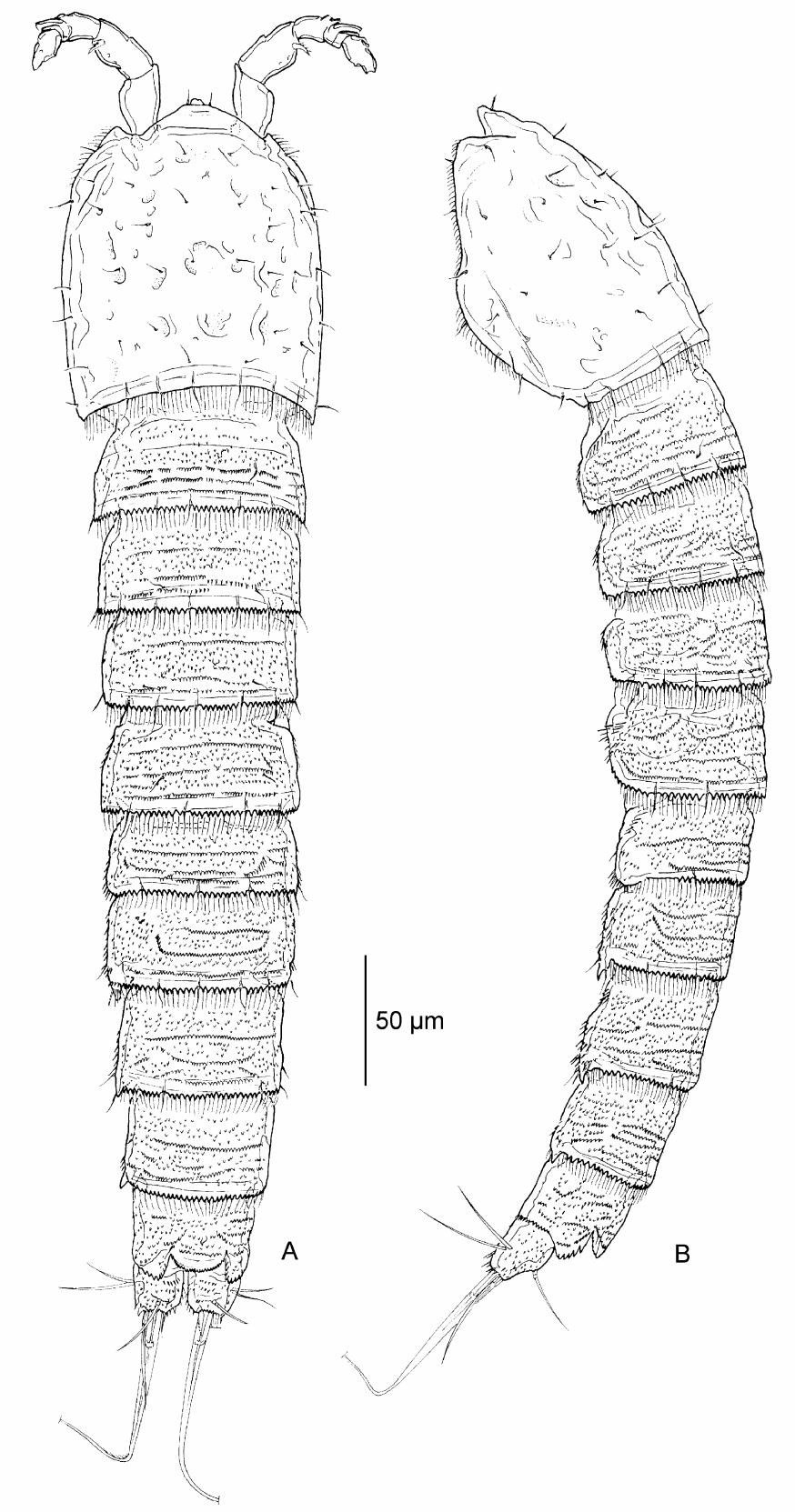


Figure 1. *Tapholeon ornatus* Wells, 1967. (A) female habitus, dorsal; (B) female habitus, lateral.

(b) Additional material: one female dissected on one slide (COP 1991), nine females and 13 males in 70% alcohol (COP 1990); all from Comoros, southeast coast of Grande Comore, Ouroveni (11° 54' S, 43° 29' E), small protected creek with mangrove, fine sand sample; collected on 3 August 1984 by Groupe Plongée de l'Expedition Karthala.

Redescription of female

Total body length 448 – 514 μm (n = 4; average = 484 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 103 μm. Measurements by Wells (1967): average length 443 μm (range 364-507 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Rostrum (Fig. 2A) well-developed, broad at base; fused to cephalothorax; with pair of sensilla anteriorly.

Habitus (Fig. 1A, B) elongate and slender, slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect; without demarcation between prosome and urosome. Cephalothorax slightly longer than wide, with parallel margins. Free prosomites and following urosomite equally wide; genital double-somite and following urosomite slightly extended laterally, resulting in posteriorly directed lateral process; urosome scarcely tapering posteriorly. Second and third urosomite fused to form genital double-somite. Genital double-somite with transverse surface ridge dorsally and laterally, indicating original segmentation; fused ventrally. Anal operculum convex with slightly serrate margin, not distinctly protruding.

Integument of cephalothorax with pattern of slight depressions; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite densely clothed irregularly with small denticles, some of which organised in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites serrate. Posterodorsal margins of cephalothorax and free somites clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite).

Ventral surface (Fig. 4A) of genital double-somite smooth. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following somites clothed with transversely arranged small denticles and spinules. Genital double-somite and following two urosomites laterally with spinules. Ventral surface of caudal rami smooth, with few small spinules laterally and two spinular rows apically. Posteroventral margins of genital double-somite and of following two urosomites slightly serrate, bearing row of slender spinules.

Caudal rami (Fig. 5G) slightly flattened; as long as broad. Dorsal surface depressed beyond implantation of seta VII. Dorsal surface covered with small denticles; inner margin bearing transversal rows of spinules along proximal half, with transversal row of strong denticles medially from seta VII. Seta I, II and III inserted near middle of outer margin; seta VII near middle of ramus. Seta IV and V not fused, both unipinnate; all other setae naked. Seta I rudimentary.

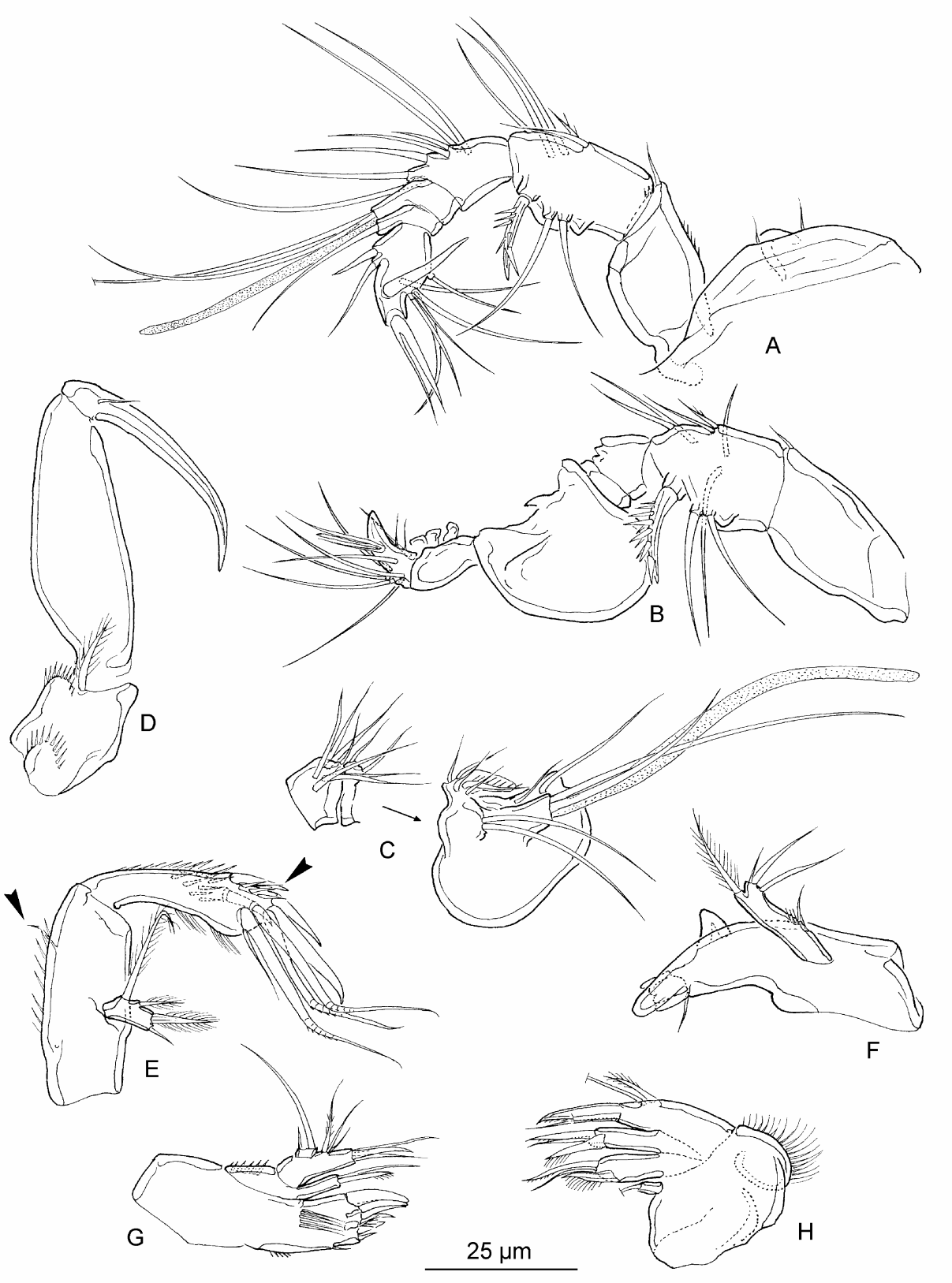


Figure 2. *Tapholeon ornatus* Wells, 1967. (A) female antennule and rostrum, dorsal; (B) male antennule (armature of segments III, IV and V omitted), dorsal; (C) male antennule (segments III, IV and V), ventral; (D) female maxilliped; (E) female antenna (abexopodal seta and small subapical seta on enp arrowed); (F) female mandible; (G) female maxillule; (H) female maxilla.

Antennule (Fig. 2A) six-segmented; suture between fourth and fifth segment faint. First segment with small spinules along anterior margin. Second segment bearing small blunt process along posterior margin. Majority of setae long and slender; second segment with strong, armed spine along outer margin; ultimate segment bearing two stout setae, one fused basally to slender seta. Armature formula: 1-[1], 2-[8], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[11]. Apical aesthetasc could not be discerned.

Antenna (Fig. 2E). Allobasis with spinular row along abexopodal side; with one minute abexopodal seta. Exp unisegmented and small, bearing one long plumose seta, two short bipinnate setae and one small naked seta. Enp with spinular rows and two subapical frills; with following armature: subapically, two spines and one small seta; apically, two strong spines, three geniculate, pinnate setae and one slender seta.

Mandible (Fig. 2F). Gnathobase formed by several blunt teeth and one seta. Palp uniramous; endopod and exopod represented by three and one smooth seta(e), respectively. Basal seta plumose.

Maxillule (Fig. 2G). Praecoxa with arthrite bearing spinular row on posterior surface, medial margin furnished with eight setae/spines. Coxal endite with one seta and one pinnate spine. Basal endite with two naked setae and one curved spine. Endopod obsolete, represented by three setae. Exopod one-segmented with two apical setae.

Maxilla (Fig. 2H). Syncoxa with three endites; with row of spinules along outer margin. Praecoxal endite small, with one seta. Both coxal endites with one strong, pinnate spine, one slender, naked and one slender, pinnate seta. Allobasis drawn out into slightly curved, distally pinnate claw; bearing two slender setae. Endopod obsolete, represented by two setae.

Maxilliped (Fig. 2D). Syncoxa with one pinnate seta and two rows of spinules. Endopod clawshaped, naked; with short naked seta at base.

P1 (Fig. 3A). Coxa with several spinular rows as figured. Basis with one pinnate seta along outer margin; medial seta arising on anterior surface; long spinules along inner and few, small spinules along outer margin and on anterior surface. Exopod two-segmented; exp-2 bearing four setae. Enp-1 4.5 times as long as exp; with few spinules along inner margin. Enp-2 with spinules along outer margin and distal inner corner; with one smooth claw and one minute, naked accessory seta.

P2-P4 (Fig. 3B, C, D). Setal formula in Table 1. Exopods three-segmented and endopods two-segmented. Prae-coxae triangular with distal row of small spinules. Coxae with rows of spinules along outer margin. Bases with spinular row near insertion place of pinnate (P2) or naked (P3-P4) basal seta. Segments of endopods and exopods with pattern of spinules as figured.

P5 (Fig. 4C) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surfaces smooth. Baseoendopod reaching to distal fourth of exopod. Basal seta arising from cylindrical setophore, with tube pore proximally and small, spinous process along outer distal margin. Proximal spines of endopodal lobe unipinnate; sub-apical and apical seta plumose. Exopod rhomboid; two times as long as wide; bearing five plumose setae.

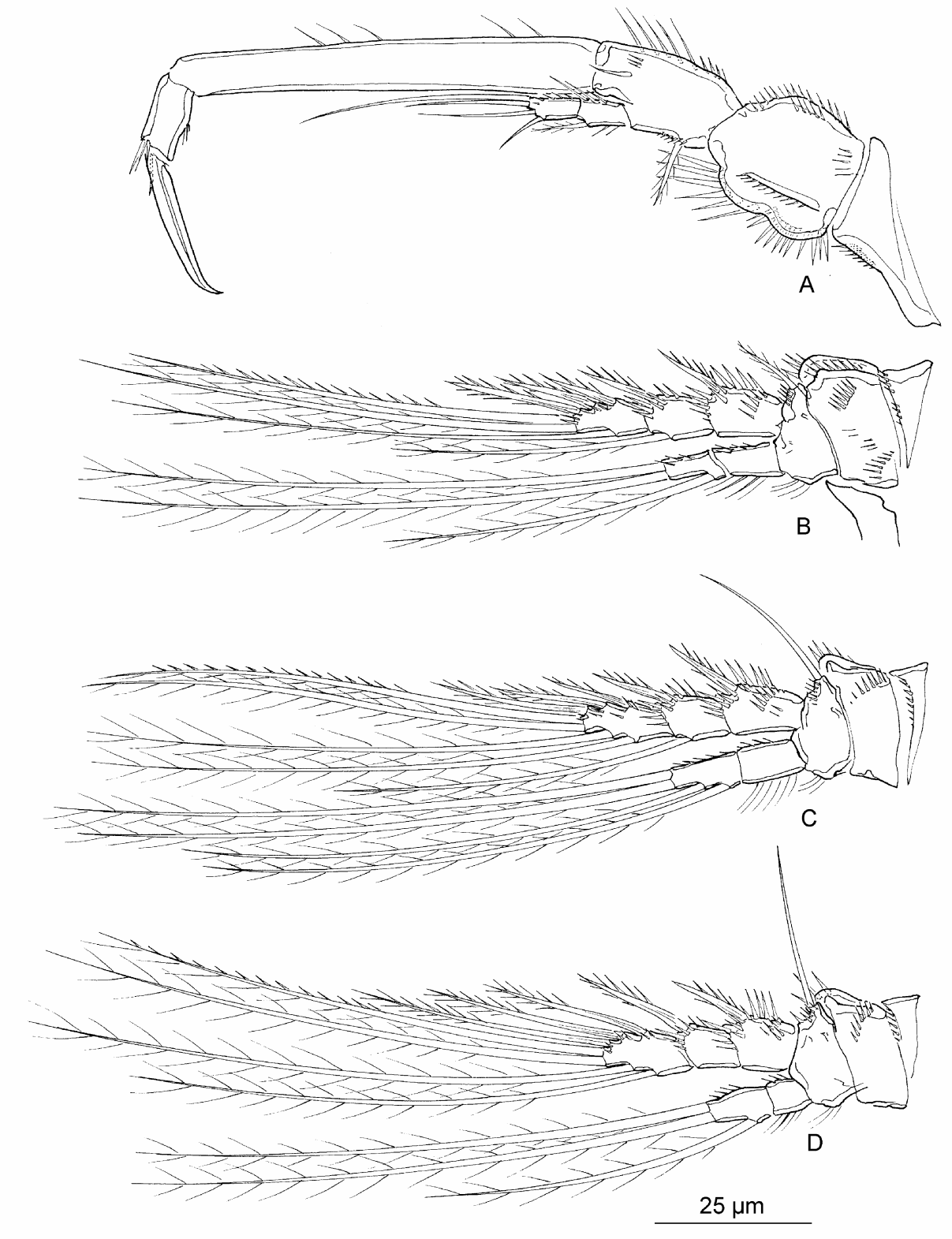


Figure 3. *Tapholeon ornatus* Wells, 1967. (A) female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior.

P6 vestige (Fig. 4A) bearing one seta.

Redescription of male

Total body length 448 – 480 μm (n = 2; average = 464 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 84 μm. Measurements by Wells (1967): average length 389 μm (range 351-468 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fifth urosomites (Fig. 4B). Ventral surface of third urosomite with several rows of spinules and small denticles.

Antennule (Fig. 2B, C) seven-segmented; sub-chirocer. Shape of first and second segment as in female. Setae on ultimate segment all slender, i.e. without any stout setae as in female. Armature formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[11 + (1 + ae)], 6-[0], 7-[9 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to two setae.

Antenna, mouthparts and P1 to P4 as in female.

P5 (Fig. 4D). Endopodal lobe of P5 obsolete; with tube pore and without seta. Basal seta on setophore, with tube pore proximally. Exopod small; slightly wider than long; bearing three plumose setae. Anterior surface with spinules.

P6 vestiges (Fig. 4B) asymmetrical. One vestige functional; one vestige fused to somite. Both produced into cylindrical process bearing one pinnate, strong inner and one naked outer seta.

Amendments – The most important amendment undoubtedly is the presence of two inner setae on exp-3 of P4, instead of one seta as mentioned by Wells (1967). The preparations of the holotype only contained the left P4 (also drawn by Wells), which clearly shows two inner setae on exp-3. Furthermore, a small abexopodal seta is present on the allobasis of the antenna. Drawings were made, based on one female (NHM 2006.1492) and one male paratype (NHM 2006.1494). All characteristics were carefully verified on the female holotype (NHM 1967.8.4.106) and the male paratype (NHM 1967.8.4.107).

Variability – The specimens from the Comoro Islands agree in all aspects with the type specimens from Mozambique.

Differential diagnosis – Species discrimination within *Tapholeon* is mainly based on the chaetotaxy of the swimming legs. *Tapholeon ornatus* bears three outer spines on the ultimate segments of the exopods of P2-P4, lacks an inner seta on exp-2 of P4 and bears three, four and three setae on the second endopodal segments of P2 to P4, respectively. Also, the pleurotergites of the body somites of this species are densely clothed with small denticles, some of which are organised in transversal rows.

Distribution – Inhaca Island, Mozambique (Wells, 1967); Grande Comore, Comoro Islands (present study).

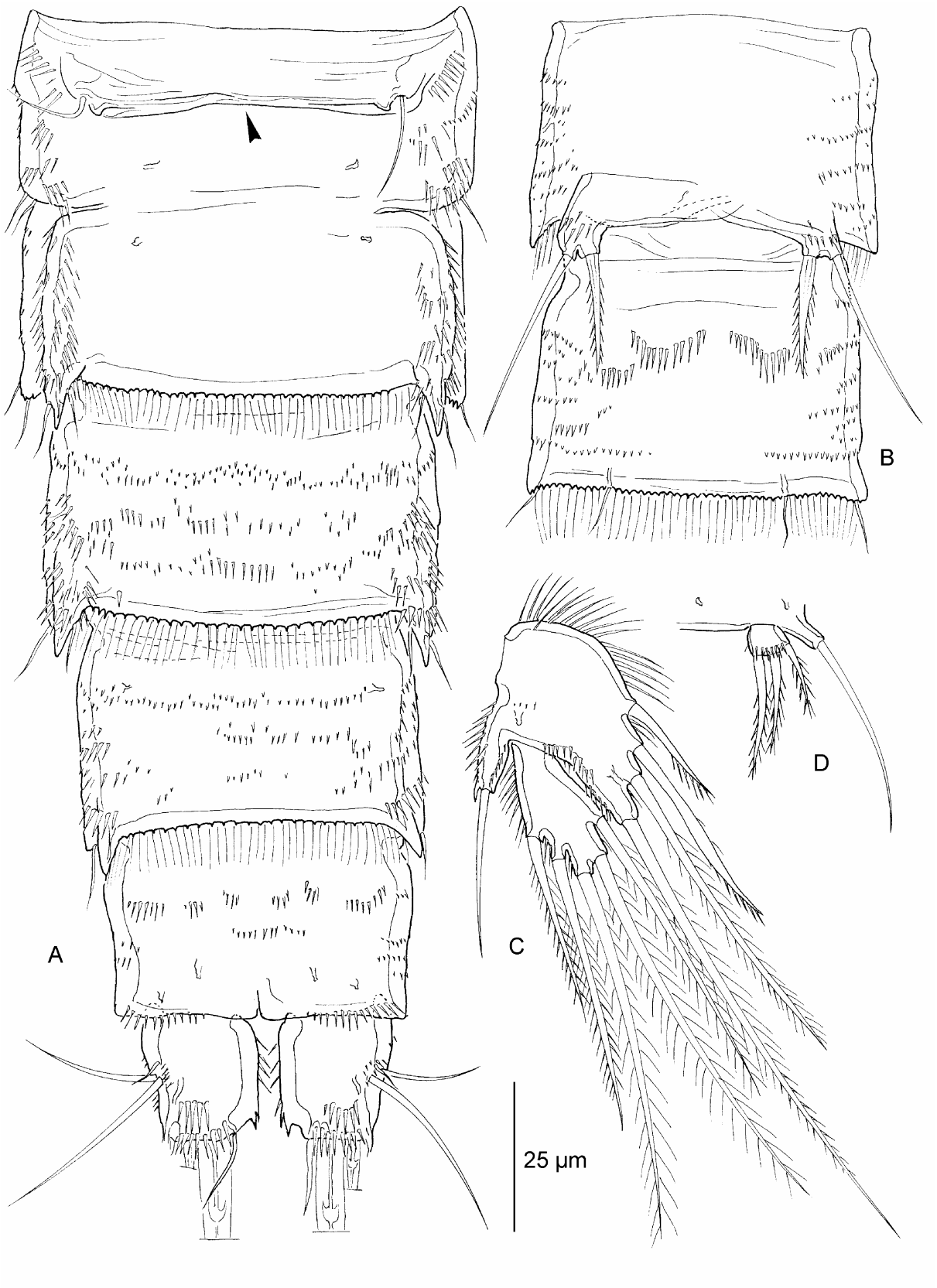


Figure 4. *Tapholeon ornatus* Wells, 1967. (A) female urosome (copulatory pore arrowed), ventral; (B) male second and third urosomite, ventral; (C) female P5, anterior; (D) male P5, anterior.

***Tapholeon arenicolus* (Chappuis, 1954) comb. nov.** (Figures 5-6)

Synonym – *Asellopsis arenicola* Chappuis, 1954

Type locality – Comoro Islands, Grande Comore (beach of Mitsamiouli), very fine coral sand, and gravel with coral rubble and shell debris (Chappuis 1954).

Type material – Unknown.

Additional material – Comoros, southeastern coast of Grande Comore, Ouroveni (11° 54' S, 43° 29' E), small protected creek with mangrove, sample of fine sand – two dissected females (COP 1984, COP 1985), one dissected male (COP 1986) and more than 50 specimens preserved in alcohol (COP 1987); collected on 3 August 1984 by Groupe Plongée de l'Expedition Karthala.

Redescription of female

Total body length 354 – 398 μm (n = 10; average = 373 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 97 μm. Measurements by Chappuis (1954): 0.4 mm without caudal setae.

Rostrum triangular and prominent; fused to cephalothorax.

Habitus (Fig. 5A). Body elongate and slender; urosome weakly tapering towards anal somite. Genital double-somite and following urosomite slightly extended laterally. Integument of cephalothorax and pleurotergites with irregular pattern of small denticles. Posterodorsal margin of cephalothorax smooth, of free prosomites smooth along median part but serrate laterally, of all urosomites serrate. Posterodorsal margins of all free somites (except second urosomite) clothed with slender hairs. Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface of genital double-somite and following urosomites smooth. Posteroventral margins of genital double-somite and of next two urosomites with long, slender hairs.

Caudal rami (Fig. 5B, C) flattened; as long as wide, with subquadrate appearance in dorsal view; tapering strongly towards apical margin in lateral view. Surface strongly concave beyond implantation of dorsal seta. Distal inner corner rounded, strongly serrate. Lateral margin spinulose. Seta IV short; seta V about two times length of caudal ramus and pinnate; all other setae naked. Seta VII inserted near middle of ramus.

Antennule (Fig. 5E) six-segmented. First, second and third segment each with row of spinules. Second segment with strong, armed spine along outer margin. Ultimate segment with rounded tip. Armature formula as in type species.

Antenna (Fig. 5F) and mouthparts as in type species.

P1 (Fig. 6A) with pattern of spinules as figured. Exopod two-segmented; exp-2 bearing four setae. Enp-1 four times as long as exp.

P2-P4 (Fig. 6B, C, D) with three-segmented exopods and two-segmented endopods, with pattern of spinules as figured. Setal formula in Table 1.

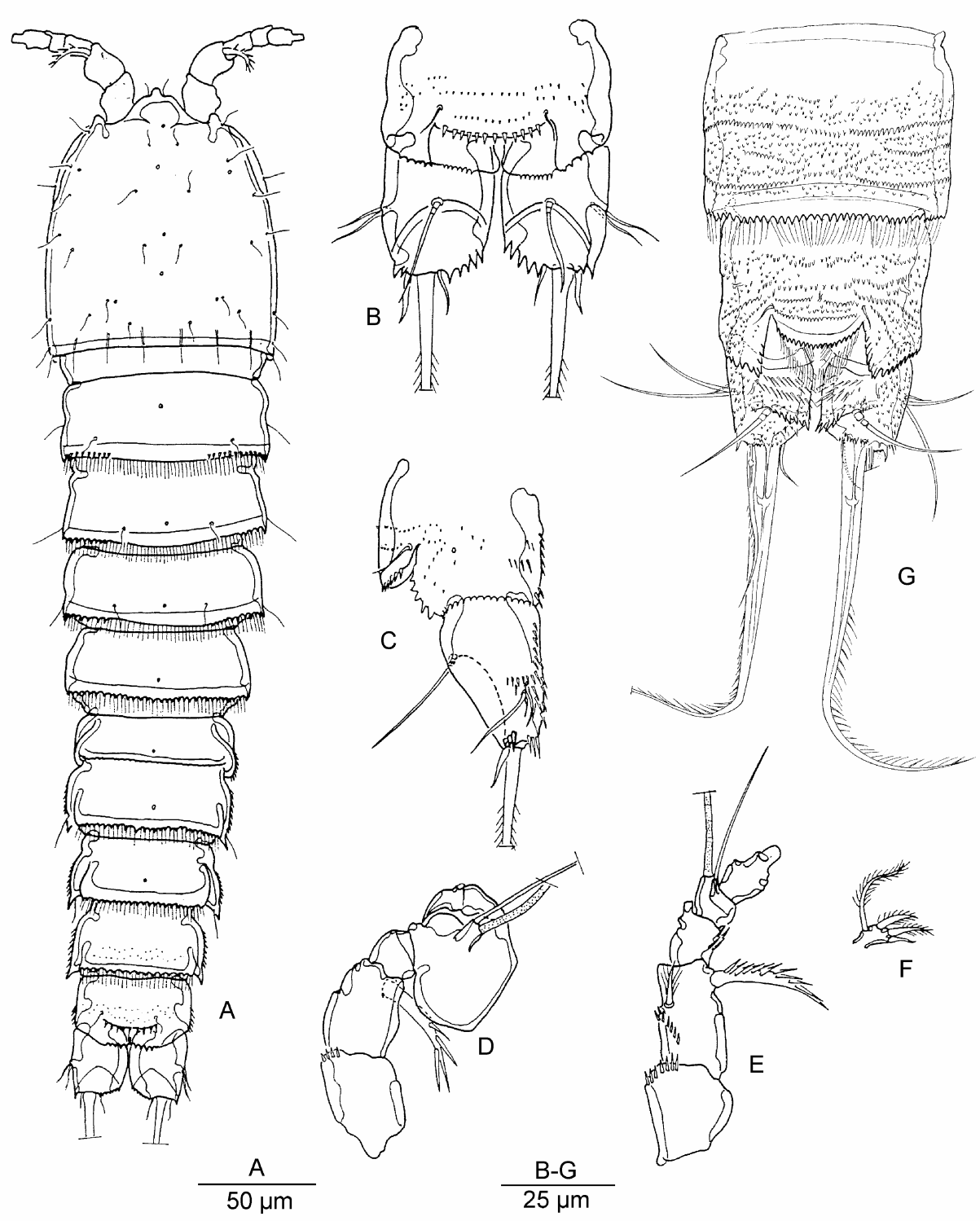


Figure 5. *Tapholeon arenicolus* (Chappuis, 1954) comb. nov. (A) female habitus, dorsal; (B) female caudal rami, dorsal; (C) female caudal rami, lateral; (D) male antennule (armature omitted), ventral; (E) female antennule (armature omitted), ventral; (F) female antennary exopod; *Tapholeon ornatus* Wells, 1967. (G) female anal somite and caudal rami, dorsal.

P5 (Fig. 6D) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surface smooth. Baseoendopod reaching beyond middle of exopod; bearing one apical and three lateral setae. Exopod ovate; two times as long as wide; bearing five setae.

P6 vestige bearing one seta.

Redescription of male

Total body length 346 – 384 μm (n = 10; average = 362 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 88 μm. Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites. Ventral surface of third urosomite with transversal row of large spinules.

Antennule (Fig. 5D) sub-chirocer. Shape of first and second segment as in female. Armature formula as in type species.

Antenna, mouthparts and P1 to P4 as in female.

P5 (Fig. 6G). Endopodal lobe obsolete; without seta. Exopod small; bearing three strongly armed setae.

P6 vestiges (Fig. 6F) asymmetrical; each bearing a plumose inner and a naked outer seta.

Remarks – Chappuis (1954) assigned this species to the genus *Asellopsis* Brady and Robertson, 1873 because of the remarkably flattened (asellopsiform) caudal rami. Also, at the time of description the genus *Tapholeon* had not been established. However, Chappuis (1954) made no reference to a three-segmented endopod P3 in the male, but only mentioned a slightly shorter inner seta on the second endopodal segment of this leg. In the present material, neither a three-segmented male endopod nor a differentiated seta was found. Therefore, *A. arenicola* should be excluded from the genus *Asellopsis*, which typically displays pronounced sexual dimorphism in the third leg. Fortunately, Chappuis (1954) illustrates the peculiar seta on the second antennular segment. The thickened antennular seta, the lack of sexually dimorphic structures in the legs and the strongly reduced shape of the P5 in the male clearly indicate that *A. arenicola* must be transferred to the genus *Tapholeon*. Other differences with the original decription are: P1 exopod with four setae on the second segment, instead of three as shown by Chappuis (1954); the much longer setae (reaching far beyond the exopod) of the endopods of P2-P4; the presence of an inner seta on exp-2 of P3 and the plumose setae on the rami of the P5.

Differential diagnosis – The present species bears three outer spines on the ultimate segments of the exopods of P2-P4, lacks an inner seta on exp-2 of P4 and bears two, three and three setae on the second endopodal segments of P2 to P4 respectively.

Distribution – Grande Comore, Comoros (Chappuis 1954; present report).

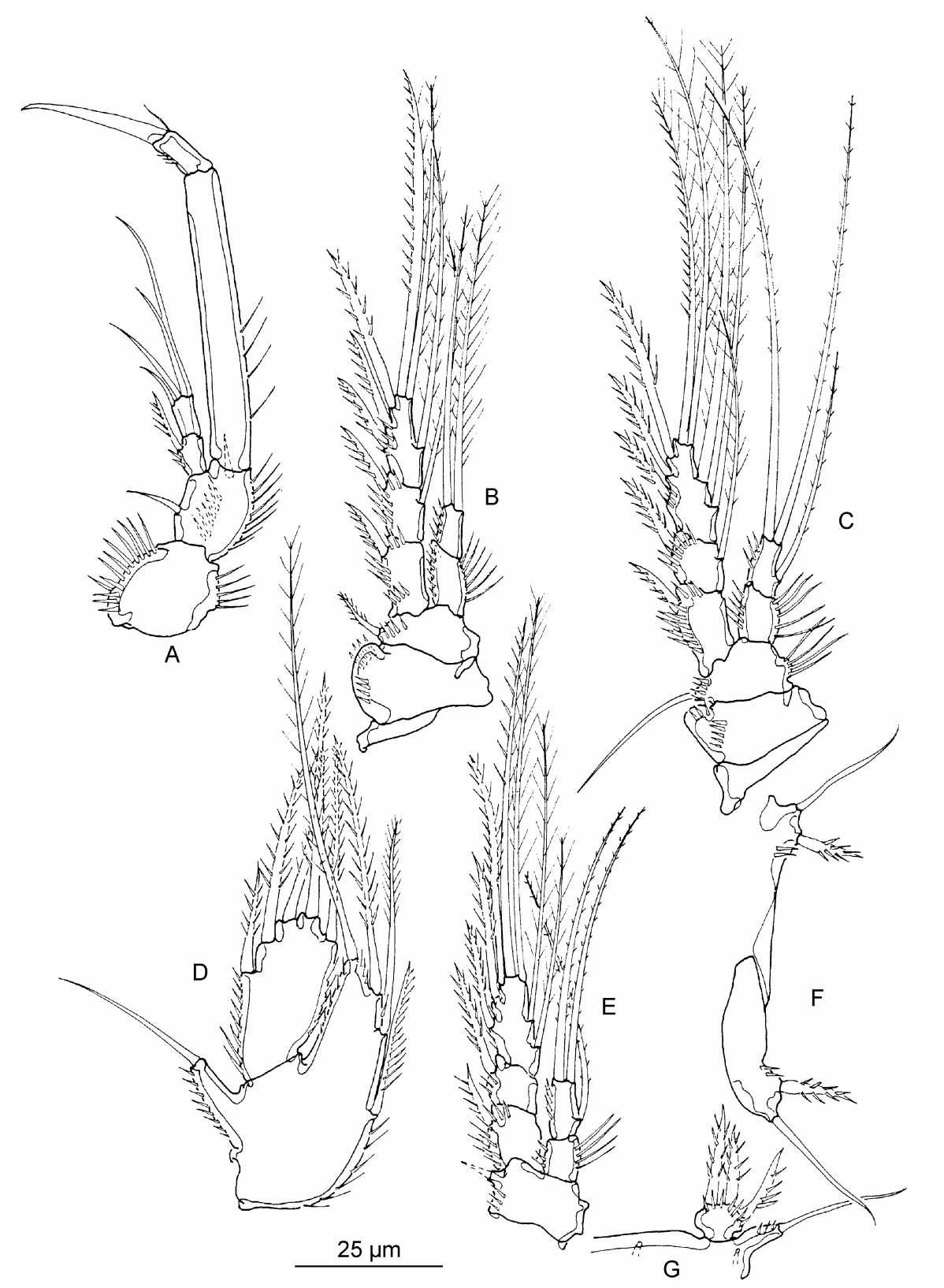


Figure 6. *Tapholeon arenicolus* (Chappuis, 1954) comb. nov. (A) female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P5, anterior; (E) female P4, posterior; (F) male P6, anterior; (G) male P5, anterior.

***Tapholeon chappuisius* (Krishnaswamy, 1957) comb. nov.**

Synonym – *Asellopsis chappuisius* Krishnaswamy, 1957

Type locality – India, Madras: Mandapam, sandy beach (Krishnaswamy 1957)

Type material – Unknown.

Diagnosis

Body strongly tapering towards caudal rami. Caudal rami slightly longer than wide. Antennule five-segmented. Antennary exopod well developed bearing three (?) setae. P1 with two-segmented exopod; exp-2 bearing three (?) setae. Exp-2 of P2-P4 with inner seta. Exp-3 of P2 with one inner seta and two outer spines; exp-3 of P3 and P4 each with two inner setae and two outer spines. Enp-2 of P2-P4 with only two apical setae each. Female P5 with four baseoendopodal and five exopodal setae. Baseoendopod reaching almost to distal margin of exopod. Exopod ovate, about two times as long as wide. Male swimming legs P1-P4 as in female. Endopodal lobe of male P5 without seta. Exopod small; bearing four setae.

Length of female: 1.2 mm (Krishnaswamy 1957), 0.56 mm (Rao and Ganapati 1969). Length of male: 0.9 to 1 mm (Krishnaswamy 1957).

Remarks – For the same reason as mentioned for *T. arenicolus* (Chappuis, 1954) comb. nov., Krishnaswamy (1957) assigned this species to the genus *Asellopsis* Brady and Robertson, 1873. However, *A. chappuisius* must be allocated to the genus *Tapholeon* because of the lack of sexual dimorphic structures in the swimming legs. The presence of an armed, strong spine on the second segment of A1 might have been overlooked. The lack of type material however prevented verifying this.

Several comments on the species description by Krishnaswamy (1957) are necessary. The antennule is described as being five-segmented. The faint suture, separating segment four and five (as seen in the type species), might have been missed and, therefore, the antennule might be six-segmented. The drawing of the exopod of the antenna shows only three setae. In the species of the genus *Tapholeon*, one seta of the antennary exopod is very slender and small, and can easily be overlooked. A much more important problem arises in the enumeration of the legs. The figure of the P4 (Krishnaswamy, 1957) undoubtedly illustrates the P2 of this species. P4 has two inner setae on the last exopodal segment in the majority of the species and never has an endopod reaching to the apical edge of the second exopodal segment. Consequently, the figure of P2 must be another leg and seems to represent P3 because: (1) the third exopodal segment bears two inner setae and (2) the endopod reaches to the middle of the second exopodal segment. The description of P2 has to be considered as the description of the P4. This amendment results in an entirely different setal formula as given in Table 1.

Most curiously, Rao & Ganapati (1969) follow Krishnaswamy (1957) in their redescription of *T. chappuisius*. However, the drawings given by Rao & Ganapati (1969, Figure 16) appear to be duplicates from the original ones.

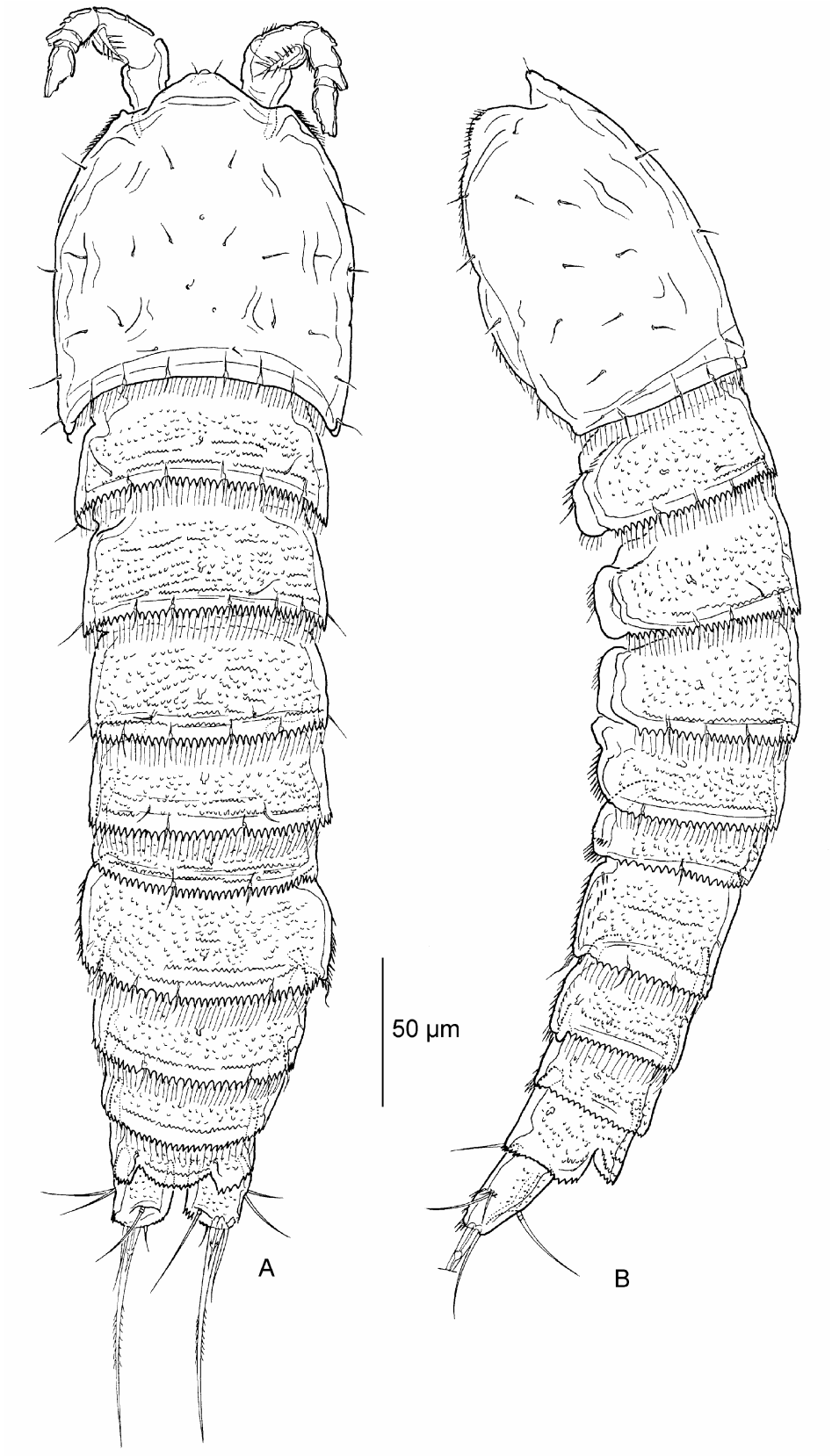


Figure 7. *Tapholeon inconspicuus* Gheerardyn & Fiers sp. nov. (A) female habitus, dorsal; (B) female habitus, lateral.

Differential diagnosis – *T. chappuisius* comb. nov. bears two outer spines on the ultimate segments of the exopods of P2-P4 and only bears two apical setae on the second endopodal segments of P2 to P4.
Distribution – Madras (Krishnaswamy, 1957) and Waltair (Rao & Ganapati, 1969), both in the Bay of Bengal.

***Tapholeon inconspicuus* Gheerardyn & Fiers sp. nov.** (Figures 7-9)

Type locality – Western Indian Ocean, Kenyan coast, Wasini Island (4° 40' S, 39° 23' E), red (terrigenous?) sediment, water depth 3 to 4 m.
Material – From type locality: one female holotype dissected on four slides (COP 4734a-d); one male allotype dissected on three slides (COP 4735a-c); one male and one female paratype preserved in 70% alcohol (COP 4736); collected on 28 February 2002 by M. Raes.
Etymology – The specific name *inconspicuus* (Latin meaning inconspicuous) refers to the low occurrence of this species in a sample with a high number of *Tapholeon tenuis* sp. nov.

Description of female

Total body length 389 – 415 μm (n = 2; average = 402 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 97 μm.

Habitus (Fig. 7A, B) elongate, somewhat more robust; slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect. Genital double-somite and following urosomite slightly extended laterally. Integument of cephalothorax smooth; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite clothed with irregular pattern of small denticles, some of which arranged in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites strongly serrate. Posterodorsal margins of cephalothorax and free somites (except second urosomite) with long slender hairs, all bearing number of sensilla (not in penultimate urosomite). Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface (Fig. 9A) of genital double-somite smooth in anterior half, bearing small spinules in posterior half. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following two urosomites with rows of small spinules. Genital double-somite and following two urosomites laterally with spinules. Anal somite ventrally smooth, laterally with few spinules. Ventral surface of caudal rami with few rows of small spinules. Posteroventral margins of genital double-somite and of following two urosomites bearing row of small spinules and clothed with long slender hairs. Posteroventral margin of anal somite with row of spinules; one pair of spinules very long (two-thirds length of caudal ramus) and flattened.

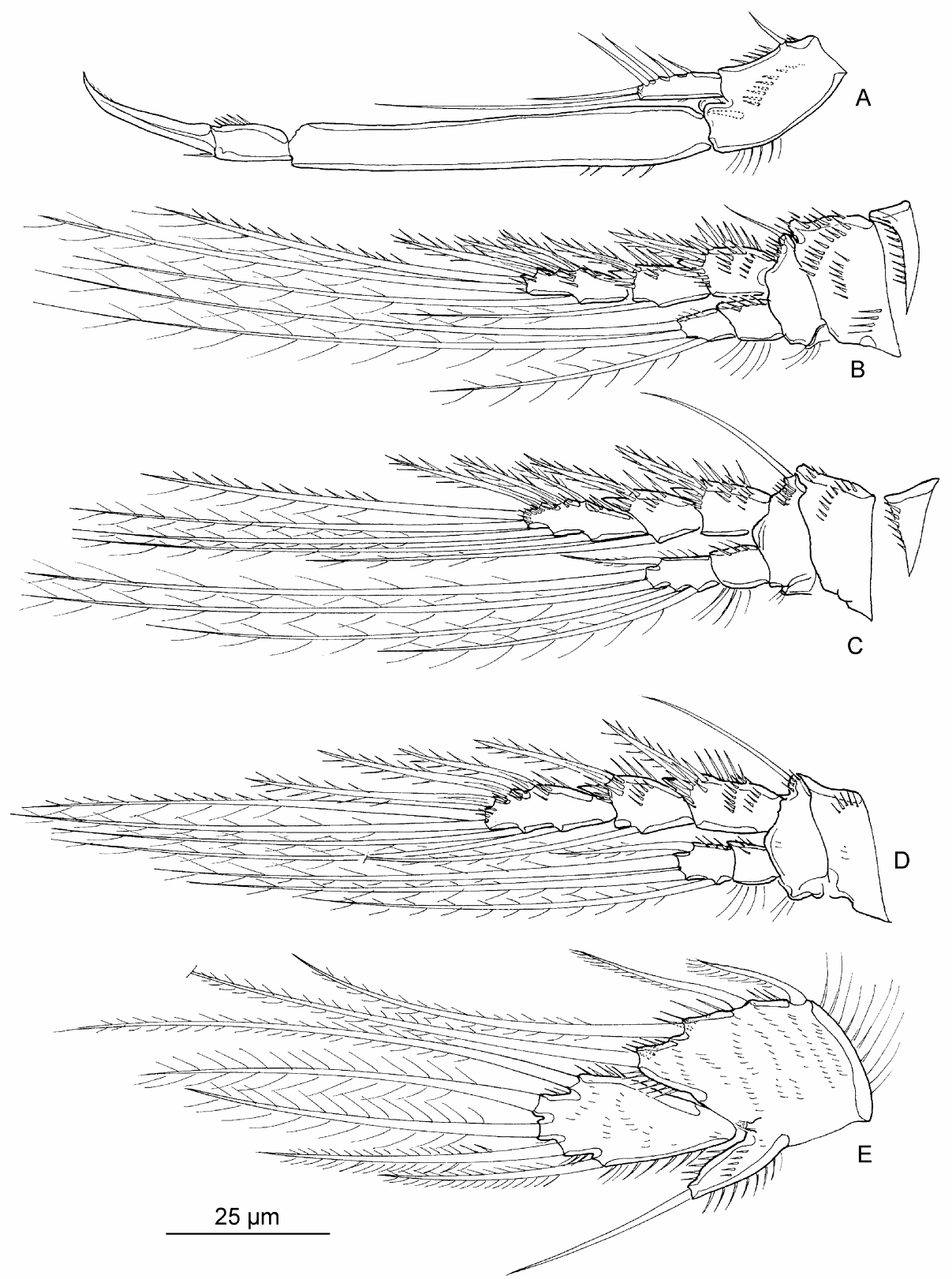


Figure 8. *Tapholeon inconspicuus* Gheerardyn & Fiers sp. nov. (A) female P1, posterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) female P5, anterior.

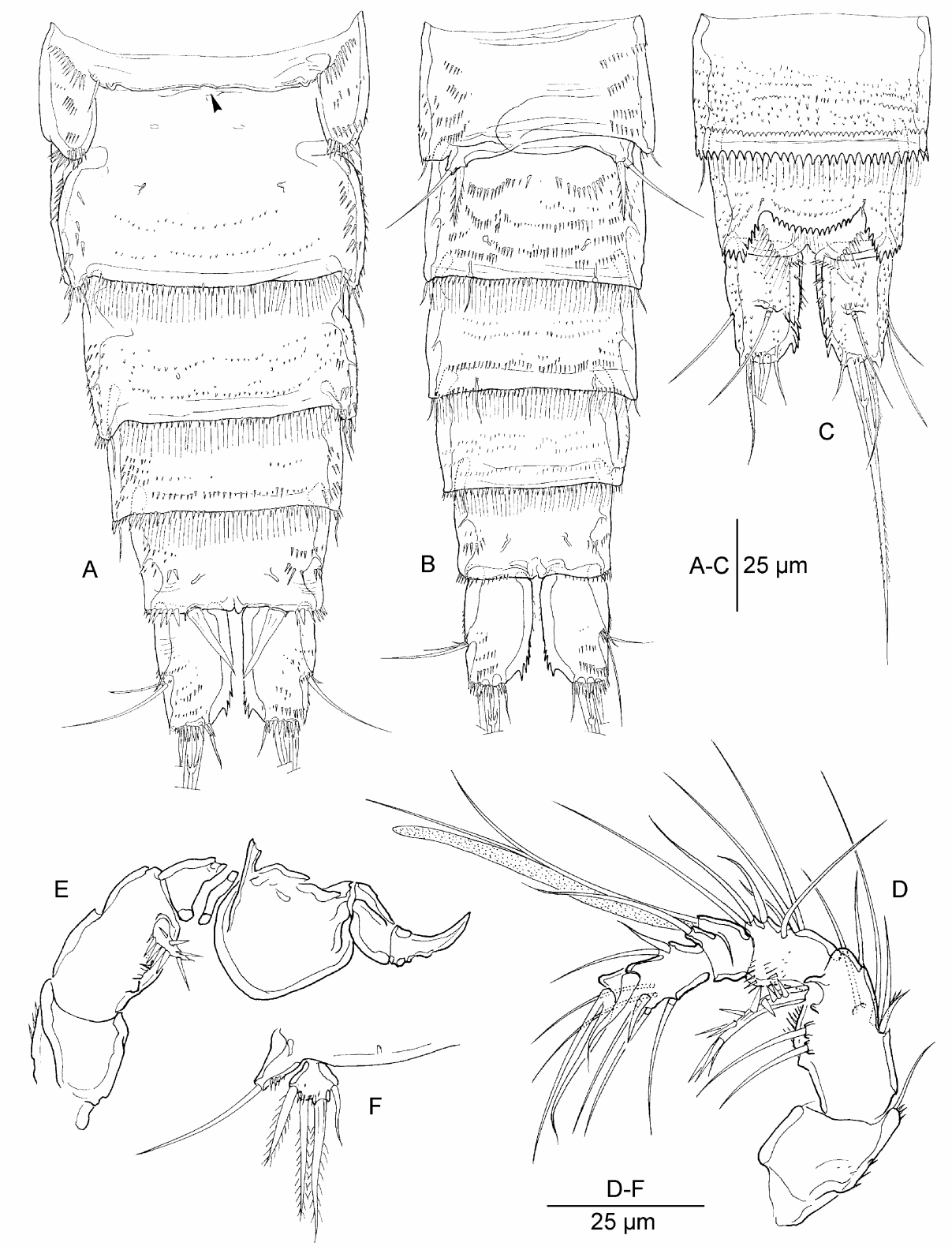


Figure 9. *Tapholeon inconspicuus* Gheerardyn & Fiers sp. nov. (A) female urosome (copulatory pore arrowed), ventral; (B) male urosome, ventral; (C) female anal somite and caudal rami, dorsal; (D) female antennule, dorsal; (E) male antennule (armature omitted), dorsal; (F) male P5, anterior.

Caudal rami (Fig. 9C) flattened; 1.5 times as long as wide; not touching each other along inner margin. Dorsal surface covered with small denticles; inner margin with small spinules along proximal half. Distal half of inner margin strongly serrate. Seta I, II and III inserted just beyond middle of outer margin, seta VII near middle of ramus. Seta IV and V not fused, both pinnate; all other setae naked. Seta I rudimentary.

Antennule (Fig. 9D) six-segmented; suture between fourth and fifth segment incomplete. Second segment bearing small blunt process along outer margin. Majority of setae long and slender; second segment with strong, armed spine near outer margin; certain setae on ultimate segment short and stout. Armature formula as in type species.

Antenna and mouthparts as in type species.

P1 (Fig. 8A). Exopod one-segmented, bearing six setae. Enp-1 five times as long as exp.

P2-P4 (Fig. 8B, C, D) with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Pattern of spinules as figured. Setal formula in Table 1.

P5 (Fig. 8E) with separate exopod and baseoendopod. Margins and surface of rami with spinules. Baseoendopod reaching to middle of exopod; bearing one apical and three lateral setae. Exopod ovate; two times as long as wide; bearing five setae.

P6 vestige (Fig. 9A) bearing one seta.

Description of male

Total body length 389 – 402 μm (n = 2; average = 396 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 84 μm.

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites (Fig. 9B). Ventral surface of third urosomite densely covered with several rows of spinules. Posteroventral margin of anal somite with row of small spinules, i.e. without pair of very long spinules as in female.

Antennule (Fig. 9E) seven-segmented; sub-chirocer. Shape of first and second segment as in female.

Antenna, mouthparts and P1 to P4 as in female.

P5 (Fig. 9F). Endopodal lobe of P5 obsolete; without seta. Exopod small; slightly wider than long; bearing one naked and three plumose seta(e).

P6 vestiges (Fig. 9B) asymmetrical; each bearing one plumose inner and one naked outer seta.

Variability – The holotype has an aberrant right P3 exopod (0.1.222). The drawing of P3 was made from the female paratype.

Differential diagnosis – The present species exhibits an unusual type of sexual dimorphism, i.e. in the female the posteroventral margin of the anal somite bears a pair of very long (two-thirds length of caudal ramus) and flattened spinules. In the male, these modified spinules are absent.

Furthermore, this species has a one-segmented exopod in P1 and bears three outer spines on the ultimate segments of the exopods of P2-P4.
Distribution – Wasini Island, Kenyan coast (present study).

***Tapholeon tenuis* Gheerardyn & Fiers sp. nov.** (Figures 10-12)

Type locality – Western Indian Ocean, Kenyan coast, Wasini Island (4° 40' S, 39° 23' E), red (terrigenous?) sediment, water depth 3 to 4 m.
Material – (a) From type locality: one female holotype dissected on four slides (COP 4737a-d); one male allotype on one slide (COP 4738); two female and three male paratypes dissected on slides (COP 4739-4743) and numerous female and male paratypes preserved in 70% alcohol (COP 4744); collected on 28 February 2002 by M. Raes.

(b) Western Indian Ocean, different locations along Kenyan coast [Diani Beach (4° 18' S, 39° 35' E), Kisite Island (4° 40' S, 39° 22' E)], coral sand, water depth from less than 0.5 m to 6 m – three female and four male paratypes (COP 4745) and seven female and 16 male paratypes (COP 4746) preserved in 70% alcohol; collected on February 2002 by M. Raes.
Etymology – The specific name *tenuis* (Latin meaning slender) refers to the slender body shape.

Description of female

Total body length 354 – 413 μm (n = 10; average = 386 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 90 μm.

Rostrum (Fig. 10A) broad triangular; fused to cephalothorax.

Habitus (Fig. 10A, B) elongate and slender; slightly dorso-ventrally depressed; with distinct convex curvature in lateral aspect. Genital double-somite and following urosomite slightly extended laterally. Second and third urosomite fused to form genital double-somite. Integument of cephalothorax with pattern of relatively large pits; regularly ornamented with small sensilla. Pleurotergites of prosomites and urosomites and dorsal surface of anal somite with irregular pattern of very small denticles. Posterodorsal margin of cephalothorax smooth, of all free somites strongly serrate. Posterodorsal margins of cephalothorax and free somites (except second urosomite) clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite). Anal operculum convex with slightly serrate margin, not protruding.

Ventral surface (Fig. 10C) of genital double-somite smooth. Copulatory pore minute, situated in middle of anterior somite. Ventral surface of following two somites each bearing two rows of very small spinules. Genital double-somite and following two urosomites laterally with spinules. Anal somite smooth ventrally, laterally with few spinules. Ventral surface of caudal rami smooth, with some spinules laterally and two spinular rows apically. Posteroventral margins of genital double-somite and of following urosomites bearing row of spinules.

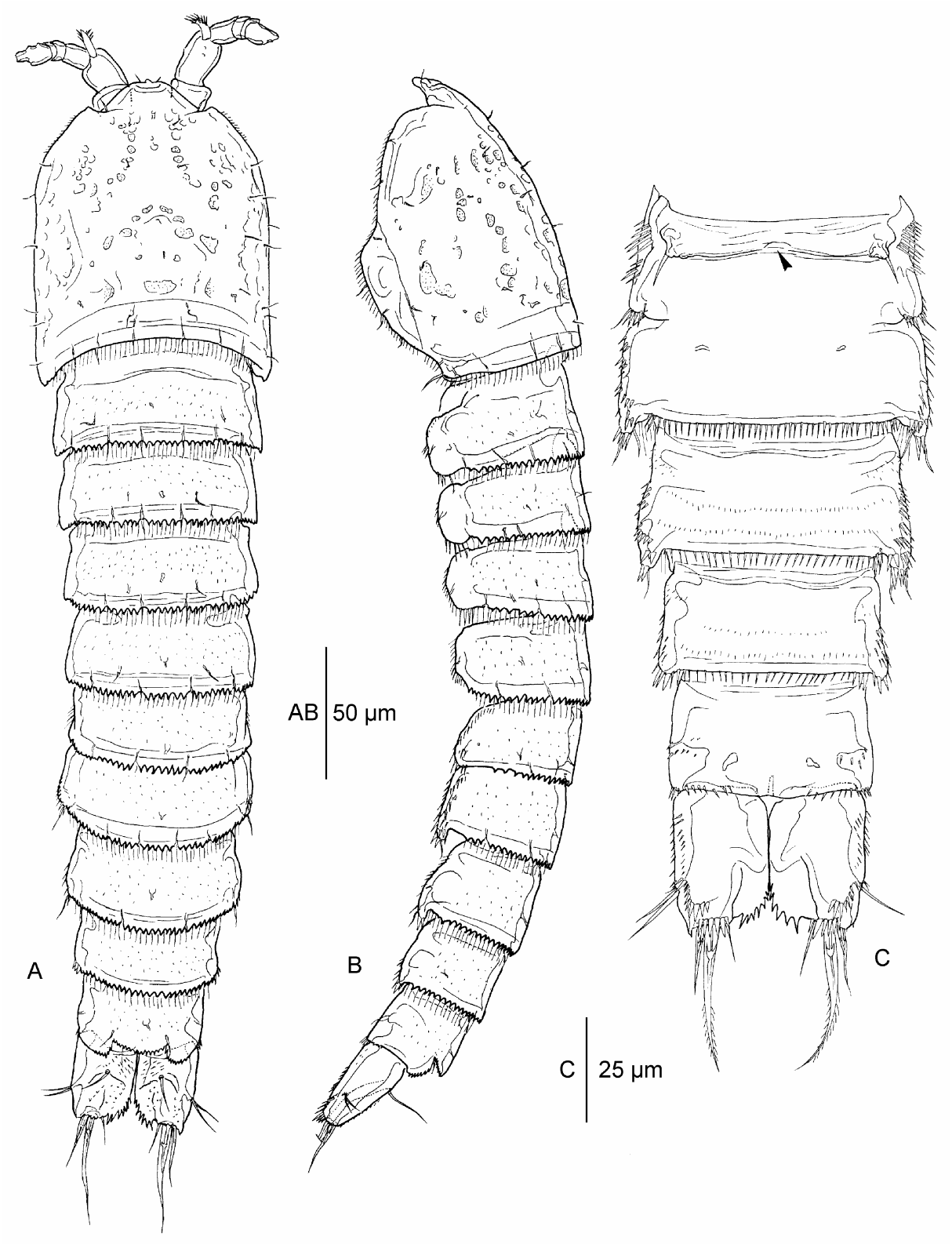


Figure 10. *Tapholeon tenuis* Gheerardyn & Fiers sp. nov. (A) female habitus, dorsal; (B) female habitus, lateral; (C) female urosome (copulatory pore arrowed), ventral.

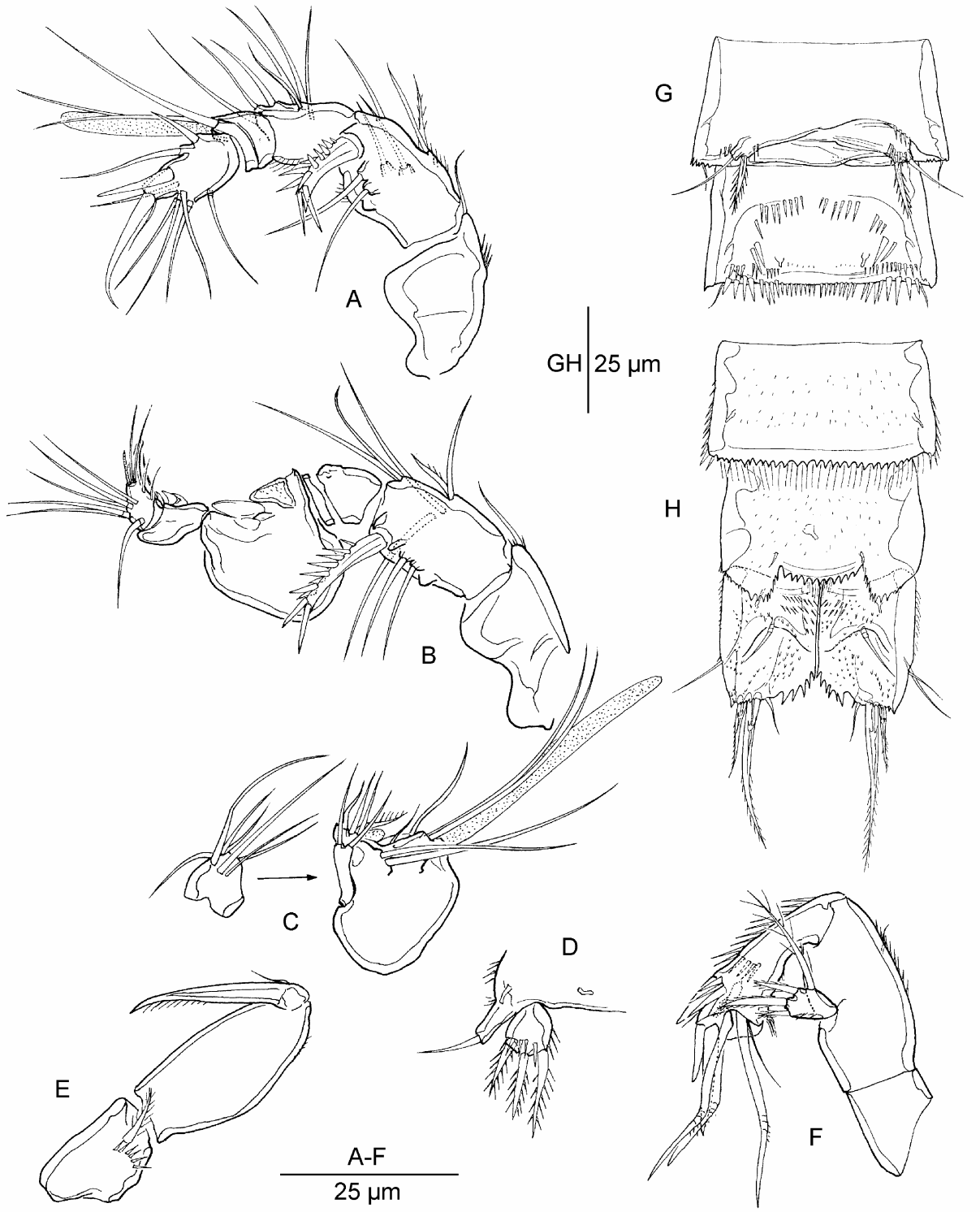


Figure 11. *Tapholeon tenuis* Gheerardyn & Fiers sp. nov. (A) female antennule, dorsal; (B) male antennule (armature of segments III, IV and V omitted), dorsal; (C) male antennule (segments III, IV and V), ventral; (D) male P5, anterior; (E) female maxilliped; (F) female antenna; (G) male second and third urosomite, ventral; (H) female anal somite and caudal rami, dorsal.

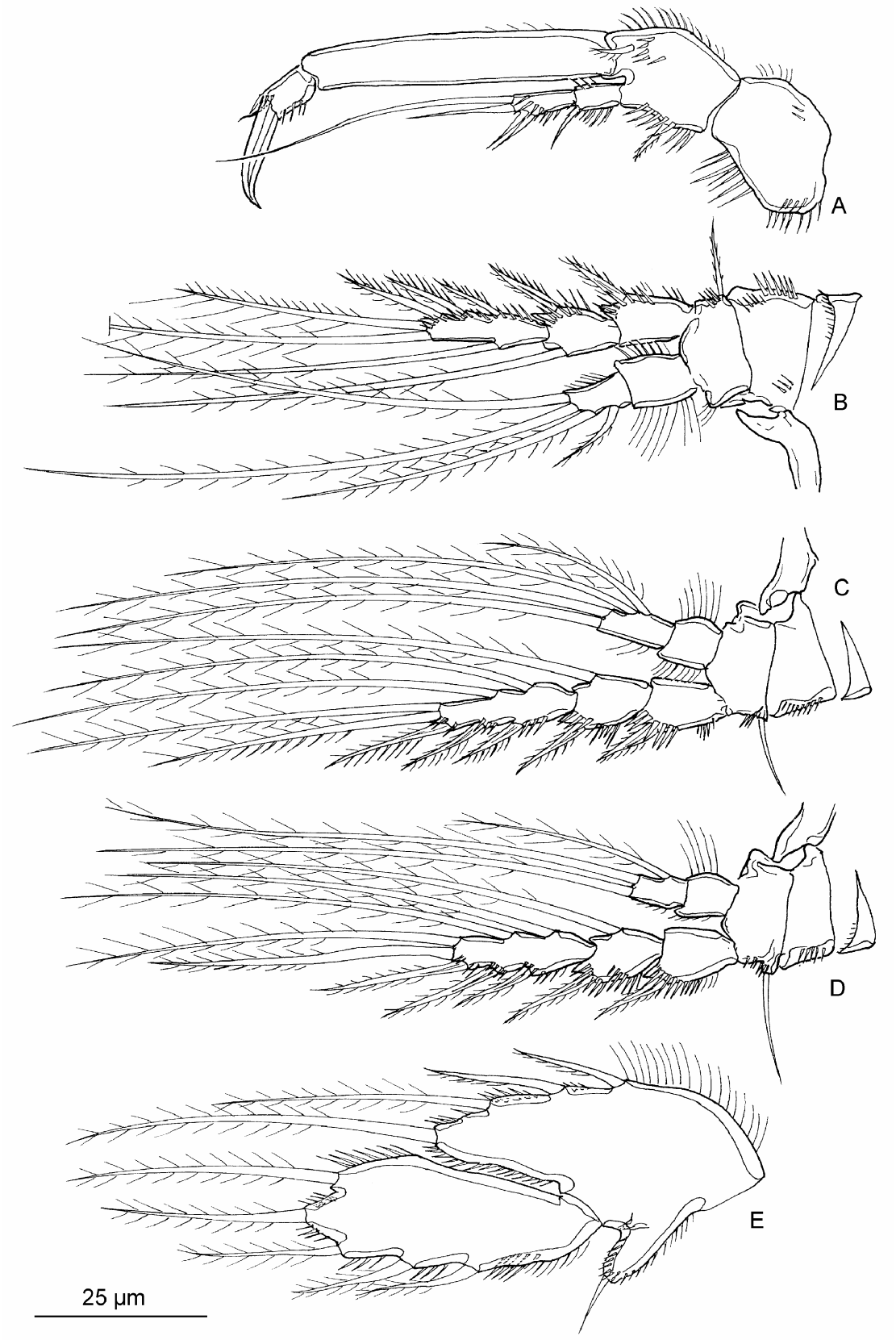


Figure 12. *Tapholeon tenuis* Gheerardyn & Fiers sp. nov. (A) female P1, anterior; (B) female P2, anterior; (C) female P3, anterior; (D) female P4, anterior; (E) female P5, anterior.

Caudal rami (Fig. 11H) flattened; slightly longer than broad; meeting each other along inner margin. Dorsal surface strongly concave beyond implantation of seta VII. Dorsal surface covered with small denticles; inner margin bearing spinules along proximal half. Distal inner corner rounded and strongly serrate. Seta I, II and III inserted in distal fourth of outer margin, seta VII near middle of ramus. Seta IV and V not fused, both pinnate and short; all other setae naked. Seta I rudimentary.

Antennule (Fig. 11A) six-segmented. First segment with spinules along anterior margin. Second segment bearing small blunt process along posterior margin, and spinules along anterior and posterior margins. Third segment with spinules along posterior margin. Majority of setae long and slender; second segment with strong, armed spine inserted near posterior margin; ultimate segment bearing two stout setae. Armature formula as in type species.

Antenna (Fig. 11F). Allobasis with one minute abexpodal seta. Exp unisegmented and small, bearing three short bipinnate setae and one long plumose seta. Armature of endopod as in type species.

Mouthparts as in type species.

Maxilliped (Fig. 11E). Syncoxa with one pinnate seta and a row of spinules. Basis with few spinules along outer margin. Endopod clawshaped, distally pinnate, with short naked seta at base.

P1 (Fig. 12A). Exopod two-segmented; exp-2 bearing four setae. Enp-1 three times as long as exp.

P2-P4 (Fig. 12B, C, D) with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Segments of endopods and exopods with pattern of spinules as figured. Setal formula in Table 1.

P5 (Fig. 12E) with separate exopod and baseoendopod. Margins of rami furnished with spinules, surface smooth. Baseoendopod reaching slightly beyond middle of exopod; bearing one apical and three lateral setae. Exopod ovate; 2.5 times as long as wide; bearing five plumose setae.

P6 vestige (Fig. 10C) bearing one seta.

Description of male

Total body length 320 – 394 μm (n = 10; average = 356 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax: 76 μm.

Habitus as in female; except for fully separated second and third urosomites and lack of lateral extensions in second to fourth urosomites (Fig. 11G). Ventral surface of third urosomite with several short rows of strong spinules.

Antennule (Fig. 11B, C) eight-segmented; sub-chirocer. Shape of first and second segment as in female. Setae on ultimate segment all slender, i.e. without any stout setae as in female. Armature formula: 1-[1], 2-[9], 3-[7], 4-[2], 5-[10(?) + (1 + ae)], 6-[0], 7-[1], 8-[8 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to two setae.

Antenna, mouthparts and P1 to P4 as in female.

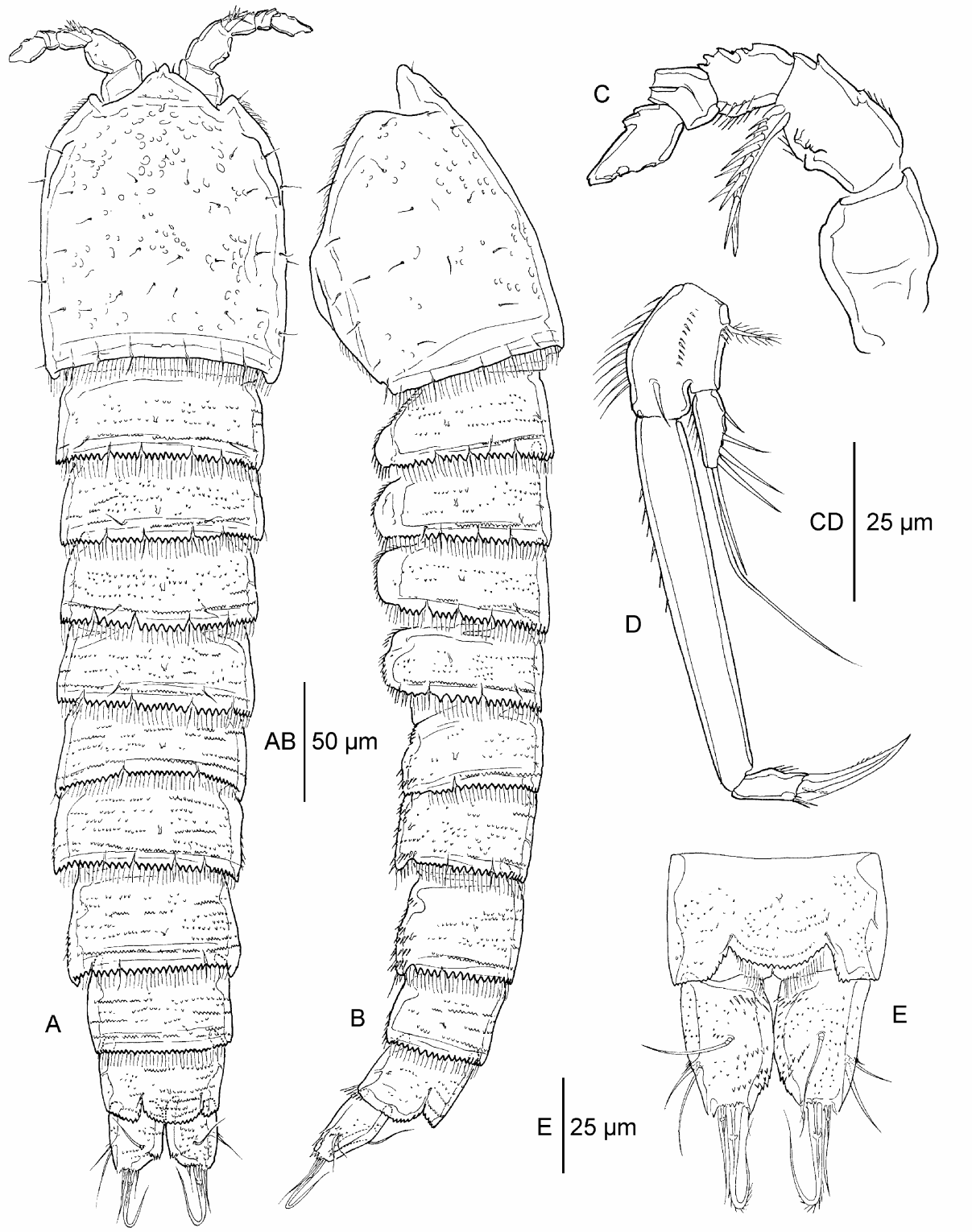


Figure 13. *Tapholeon uniarticulatus* Wells, 1967 (A) female habitus, dorsal; (B) female habitus, lateral; (C) female antennule (armature omitted), dorsal; (D) female P1, anterior; (E) female anal somite and caudal rami, dorsal.

P5 (Fig. 11D). Endopodal lobe of P5 obsolete; without seta. Exopod small; about as long as wide; bearing three plumose setae. Inner margin and anterior surface with spinules.

P6 vestiges (Fig. 11G) asymmetrical; each bearing one plumose, strong inner and one naked outer seta.

Variability – Some male and female paratypes have a right or left P2 enp with an aberrant setal formula (0.120), the opposite side consistently having a normal setal formula. Two female paratypes were found with an aberrant right and left P2 enp (0.120). One female paratype bears an aberrant P3 enp (0.120) on the left side; one other female paratype has an aberrant P3 exp (0.1.123) on the left side.

Differential diagnosis – The present species bears three outer spines on the ultimate segments of the exopods of P2-P4 and bears four, four and three setae on the second endopodal segments of P2 to P4, respectively.

Distribution – Different locations along the Kenyan coast (present study).

***Tapholeon uniarticulatus* Wells, 1967** (Figure 13)

Type locality – Mozambique, Inhaca Island: Marine Station beach (detritus sand and grass) and off Barriera Vermelha beach (detritus sand) at a depth of 5 m (Wells, 1967).

Type material – Types are deposited in the collections of the British Museum of Natural History, London (Wells, 1967).

Material examined – Type material: one female paratype dissected on six slides (NHM 2006.1495), two female and one male paratype in 70% alcohol (NHM 1967.8.4.113).

Diagnosis

Body shape (Fig. 13A, B) and proportions as in type species. Body somites scarcely clothed with irregular pattern of small denticles, some of which organised in transversal rows. Posterodorsal margin of cephalothorax smooth, of all free somites serrate. Posterodorsal margins of cephalothorax and free somites clothed with slender hairs, all bearing number of sensilla (not in penultimate urosomite). Caudal rami (Fig. 13E) flattened; 1.5 times as long as wide; inner margin slightly convex. Seta IV and V rather short. Antennule (Fig. 13C) six-segmented; suture between fourth and fifth segment incomplete. Armature formula as in type species. Second segment with strong, armed spine along outer margin. Antenna and mouthparts as in type species. P1 (Fig. 13D) with one-segmented exopod, bearing six setae. Swimming legs P2-P4 with three-segmented exopods and two-segmented endopods. Exp-1 and exp-2 equal in length; exp-3 slightly longer. Setal formula in Table 1. Female P5 with four baseoendopodal and five exopodal setae. Baseoendopod almost reaching to middle of exopod. Male swimming legs P1-P4 as in female. Endopodal lobe of male P5 obsolete; without seta. Exopod small; bearing three pinnate and one naked seta(e).

Total body length of female 469 – 470 μm (n = 2; average = 470 μm), of male 398 – 405 μm (n = 2; average = 402 μm; measured from anterior margin of rostrum to posterior margin of caudal rami). Largest width measured at posterior margin of cephalothorax of female 107 μm, of male 84 μm. Measurements by Wells (1967): average length of female 395 μm (range 351-481 μm), of male 348 μm (range 305-396 μm) (measured from base of rostrum to distal edge of last somite, thus excluding caudal rami).

Remark – Although Wells (1967) describes the P1 exopod as having five setae, his drawing of six setae is correct.

Differential diagnosis – *T. uniarticulatus* bears two outer spines on the ultimate segments of the exopods of P2-P4 and bears three, four and four setae on the second endopodal segments of P2 to P4, respectively. Also, the P1 has a one-segmented exopod.

Distribution – Inhaca Island, Mozambique (Wells 1967).

Key to the species of *Tapholeon* Wells, 1967

1. Exp-3 of P2-P4 each with two outer exopodal spines 2
   Exp-3 of P2-P4 each with three outer exopodal spines 3
2. Enp-2 of P2-P4 each bearing two setae; exopod P1 two-segmented .....
   .....*Tapholeon chappuisius* (Krishnaswamy, 1957) comb. nov.
   Enp-2 of P2-P4 bearing three, four, four setae, respectively; exopod P1 one-segmented .....
   .....*Tapholeon uniarticulatus* Wells, 1967
3. Exp-2 of P4 with inner seta 4
   Exp-2 of P4 without inner seta 5
4. Enp-2 of P2-P4 bearing three, five, four setae, respectively .....
   .....*Tapholeon inconspicuus* sp. nov.
5. Enp-2 of P2-P4 bearing four, four, three setae, respectively.....
   .....*Tapholeon tenuis* sp. nov.
6. Enp-2 of P2-P4 bearing two, three, three setae, respectively.....
   .....*Tapholeon arenicolus* (Chappuis, 1954) comb. nov.
7. Enp-2 of P2-P4 bearing three, four, three setae, respectively.....
   .....*Tapholeon ornatus* Wells, 1967

8.5. DISCUSSION

The laophontid genus *Tapholeon* was established by Wells (1967) to accommodate two new species: *T. ornatus* Wells, 1967 and *T. uniarticulatus* Wells, 1967, both from Inhaca Island (Mozambique). Since then, no new species were added and, to our knowledge, the two species have not been reported again. Wells (1967) established this genus mainly based on the absence of sexual dimorphism in the natatorial legs. In addition, the following characters form a series of apomorphic features clearly defining this taxon: the elongate and slender, but depressed body, the flattened (not cylindrical) caudal rami, the strong and armed spine on the second segment of the antennule, the reduced antennary allobasal seta and the reduced male P5, with an obsolete endopodal lobe without setae and a small exopod bearing three or four setae.

Within the Laophontidae, the genera *Asellopsis* Brady & Robertson, 1873 and *Tapholeon* are easily recognisable by their lamelliform caudal rami and typical, depressed body shape (although species of *Tapholeon* are more slender and lack well developed epimeral plates). However, *Asellopsis* can clearly be distinguished from *Tapholeon* by the distinct sexual dimorphism in the endopod of the third leg, i.e. three-segmented with an apophysis on the second segment (except in *A. intermedia* (T. Scott, 1895), in which the male P3 endopod only shows a modified chaetotaxy, as pointed out by Bodin (1970)). In the present study, additional material of the species *Asellopsis arenicola* Chappuis, 1954 revealed the absence of any sexual dimorphism in the swimming legs. Therefore, this species must be assigned to *Tapholeon*. A second species, *A. chappuisius* Krishnaswamy, 1957, also from the Indian Ocean, is assigned to this genus for the same reason.

As a consequence of the transfer of these two species, the genera *Asellopsis* and *Tapholeon* have rather distinct distributions (Fig. 14). *Asellopsis* has frequently been reported from various localities in the Mediterranean Sea (including the Black Sea) and along the eastern shores of the North Atlantic Ocean (e.g. Lang, 1948; Noodt, 1955; Por, 1959, 1964a; Griga, 1963; Guille & Soyer, 1966; Marinov, 1971; Mielke, 1975; Bodiou, 1980; Gee & Warwick, 1984), and mostly occurs in sandy and muddy bottoms. The only representative from the western shore of the North Atlantic Ocean is *A. littoralis* Nicholls, 1940, described from the shore of the River St. Lawrence (at Trois-Pistoles) (Nicholls, 1940). The type locality of *A. intermedia*, at Franz-Josef Land in the Arctic Ocean (T. Scott, 1898), represents the most northern limit of the genus *Asellopsis*. The genus *Tapholeon* (now containing six species) shows a limited distribution confined to the southwestern part of the Indian Ocean (Mozambique, Kenya, Comoros) and the Bay of Bengal. The occurrence of *T. chappuisius* comb. nov. in the Bay of Bengal might indicate a much wider distribution of *Tapholeon* in the Indian Ocean. Apart from the report of *T. arenicolus* comb. nov. in a sample of gravel with coral rubble and shell debris (Chappuis, 1954), all six species have been found in sediments (Chappuis, 1954; Krishnaswamy, 1957; Wells, 1967; Rao & Ganapati, 1969; present report). The distinct differences in sexual dimorphism and the remote distribution of *Tapholeon* and *Asellopsis* are indications that the strong resemblances in body shape and form of

the caudal rami are the result of convergence and that the two genera are not directly related to each other. Therefore, body shape and caudal rami might have evolved similarly in response to similar environmental conditions, i.e. the similar substrate in which members of both genera are found.

Figure 14. Sampling locations of the presently known species of *Tapholeon* Wells, 1967 and *Asellopsis* Brady and Robertson, 1873, based on the original descriptions and the reports in Lang (1948) and Bodin (1997). (1) *Tapholeon arenicolus* (Chappuis, 1954); (2) *T. chappuissius* (Krishnaswamy, 1957); (3) *T. inconspicuus* Gheerardyn & Fiers sp. nov.; (4) *T. ornatus* Wells, 1967; (5) *T. tenuis* Gheerardyn & Fiers sp. nov.; (6) *T. uniarticulatus* Wells, 1967; (7) *Asellopsis bacescui* Por, 1959; (8) *A. duboscqui* Monard, 1926 (■); (9) *A. hispida* Brady & Robertson, 1873 (▲); (10) *A. intermedia* (T. Scott, 1895) (●); (11) *A. littoralis* Nicholls, 1940; (12) *A. penicillata* Por, 1964; (13) *A. sarmatica* Jakubisiak, 1938.

The flattened caudal rami also occur in two species of *Paralaophonte* Lang, 1944 (i.e. *P. asellopsiformis* Lang, 1965 and *P. aenigmaticum* Wells, Hicks & Coull, 1982). Furthermore, their body shape is typical asellopsiform and quite unlike other species of *Paralaophonte*, as stated by Wells *et al.* (1982). These two species however are typical members of the genus *Paralaophonte* as illustrated by the dimorphic features in P2 and P3. Lang (1965) ascribes the similarities with *Asellopsis* to ecological convergence, as *P. asellopsiformis* (and *P. aenigmaticum*) are sediment dwellers in substrata

similar to those inhabitated by species of *Asellopsis*. Wells *et al.* (1982) however warn that a thorough phylogenetic analysis is still necessary before the homogeneity of *Paralaophonte* can be addressed.

Apart from the flattened caudal rami and the characteristic body shape, *P. asellopsiformis* and *P. aenigmaticum* furthermore bear a thickened seta on the second antennular segment. These shared characteristics might indicate a strong affinity of *Tapholeon* with *Paralaophonte*. However, *Tapholeon* is clearly differentiated by the lack of sexually dimorphic features in the endopods of P2 and P3 and the exopods of P2 to P4. Whether the similarities have to be attributed to a shared ancestry or to convergence has to be decided on the basis of a thorough phylogenetic analysis.

8.6. ACKNOWLEDGEMENTS

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CHAPTER 9

General discussion and future perspectives

9.1. HARPACTICOID COPEPODS ASSOCIATED WITH CORAL SUBSTRATES

Community structure

The physical and biological breakdown of both tropical and cold-water coral skeletons results in a large variety of substrates with different structural complexity, providing a wide range of potential microhabitats for benthic fauna. The major aim of the present study was to evaluate the role of microhabitat type in structuring community composition and diversity of the associated harpacticoid copepods. Meiofauna research has generally focused on soft-bottoms, and mostly neglected the meiofauna on hard substrates, due to their small size and sampling difficulties (Coull *et al.*, 1983; Gibbons, 1988a,b; Danovaro & Fraschetti, 2002). The few studies dealing with meiofauna and more in particular harpacticoid copepods, occurring as epifauna on a substrate, have focused on the phytal assemblages of seagrasses and macroalgae. However, the hard coral substrates, which are the subject of this study, also provide an epifaunal habitat contrasting to the infaunal habitat of the surrounding sediment.

In the shallow sublittoral of a tropical lagoon, coral fragments sustained a specific assemblage composed of typical epibenthic or even 'phytal' taxa with an addition of sediment dwellers. It is assumed that the sediment trapped by the coral fragments provides a habitat for sediment-bound taxa, while the complex microtopography of the coral branches is a suitable substratum for true epibenthic or even 'phytal' harpacticoids. The rough surface of the coral skeleton could particularly favour copepods adapted by strongly prehensile maxillipeds and first legs for efficient clinging. The different copepod composition of the microhabitats has to be attributed to differences in contributions of the taxa that are present. The coral assemblage was not composed of unique and specific families or genera restriced to this microhabitat, as is often found on algae or hard substrates (containing low levels of deposited sediments) which are distinct or even non-overlapping from often closely adjacent sedimentary habitats (Hicks, 1985; Atilla *et al.*, 2003).

In the cold-water coral degradation zone, differences in assemblage structure between the examined microhabitats were less clear. In deep-sea studies however it is a common problem that the circumstances of low animal abundance and high diversity make it particularly difficult to detect spatial changes in community structure. The high evenness, typically found in the deep sea, in combination with the limited sample sizes undoubtedly influences the observed pattern. Rose *et al.* (2005) rightly stressed the need of more extensive sampling and the use of specific sampling designs to get more representative counts of Harpacticoida from the deep sea. Apart from some subtle differences, it appears that cold-water coral fragments and underlying sediment do not harbour distinctly different copepod assemblages. Several factors might be important in explaining this pattern. As with the tropical coral fragments, the sediment retained between the coral branches might provide a habitat for typical sediment-dwellers which could obscure the presence of real epibenthic taxa. Furthermore, both in the tropics and the deep sea, the close contact between the upper sediment layer and the overlying epibenthic structure might facilitate

considerable exchange of harpacticoids. Copepods typically reside in the upper sediment layers and many are good swimmers, capable of active emergence (Fleeger, 1980; Palmer, 1988; Walters & Bell, 1994; Thistle, 2003a), although this behaviour has yet to be recorded in deep-sea environments. Also, Palmer (1988) suggested that the presence of epibenthic structure probably enhances active emergence. The presence of coral structures as an additional source and sink for emerging copepods increases the complexity of possible linkages. It should be taken into account that the high mobility of certain harpacticoids enables the exploration of different microhabitats. Hicks & Coull (1983) stated that epibenthic species, with their ability to swim, might be expected to perceive the habitat as more fine-grained (*sensu* Jumars, 1975) and be less restricted to a particular microhabitat. The apparent lack of differences in assemblage structure might also partly be due to the sampling method used. The protrusion of the boxcorer through the cold-water coral fragments might have disturbed associated meiofauna and obscured the fine patterns of habitat utilization. Although comparison is limited, the subtle differences between coral and sediment assemblage (e.g. by the higher abundance of Tetragonicipitidae in the sediment) and the presence of taxa with typical 'phytal' morphology (with prehensile first legs and modified body shapes) nevertheless indicate that the hard biogenic substrates provide a specific epifaunal habitat in contrast to the typical soft-bottom deep sea.

When comparing family composition of sediment and dead coral fragments in the tropical lagoon of Zanzibar and the deep sea of the Porcupine Seabight, it becomes clear that both regions harbour different faunas and that the distinction between coral and sediment is more clear in the tropical lagoon (Fig. 1). Tropical coral fragments are characterised by high abundance of Ectinosomatidae, Laophontidae and the phytal families Dactylopusiidae and Tisbidae, while the coral sand is distinguished by the dominance of Paramesochridae and Tetragonicipitidae. In the tropical lagoon, a large variety of habitat types (such as seagrasses, fossilized coral reef, seaweed farms) occurs and these habitats might supply the phytal and epibenthic taxa, that are present on the coral fragments. In the deep-sea environment, the number and occurrence of different habitat types is much more limited. Cold-water coral degradation zones likely have to be considered as habitat islands in the soft-bottom deep sea. Most of the associated fauna probably is recruited from these surrounding soft sediments and this might explain the lack of difference between sediment and coral assemblage. Families, as Ameiridae, Argestidae, Ectinosomatidae, Miraciidae and Pseudotachidiidae, are typically dominant in the soft-bottom deep sea, and are also important in the examined microhabitats of the cold-water coral degradation zone. Certain families, with a preference for deep-sea habitats (e.g. Argestidae, Neobradyidae, Pseudotachidiidae and Zosimidae), were only found in the Porcupine Seabight and were absent in the tropical lagoon. The phytal families Dactylopusiidae and Tisbidae are very rare in the deep sea (Seifried, 2004) and were restricted to the tropical lagoon. Several families (Ameiridae, Ectinosomatidae, Miraciidae), are important in both regions, but these taxa, however, are abundant in all marine habitats and are also important in any deep-sea study.

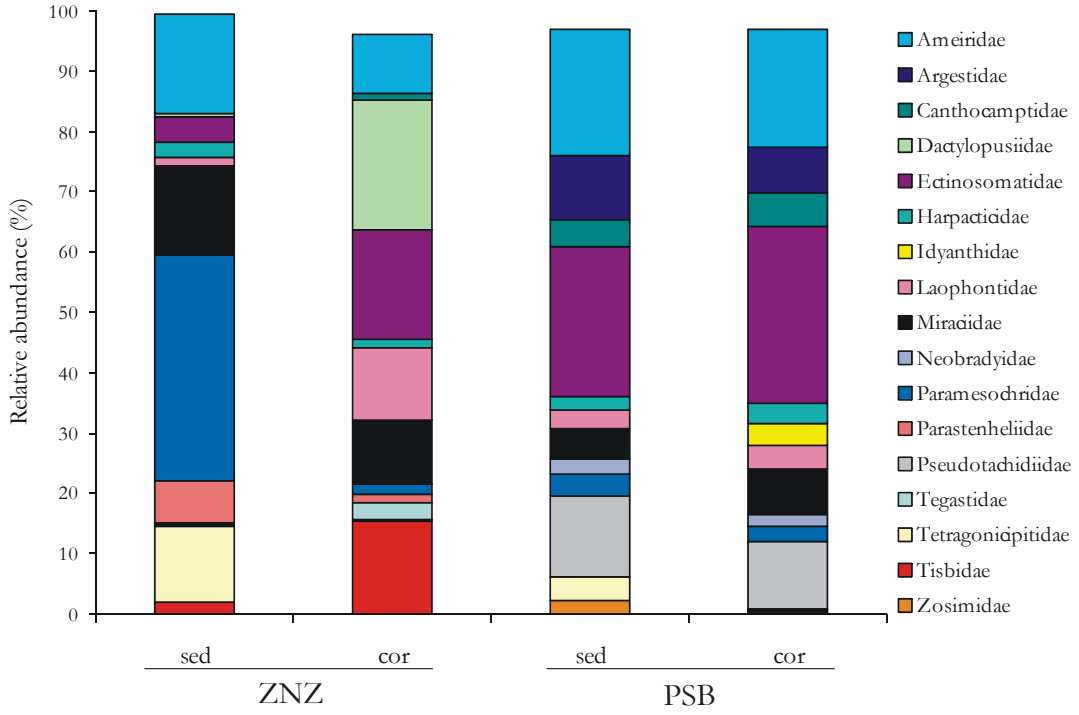

Figure 1. Harpacticoid family composition per microhabitat (sed: sediment, cor: coral) in the tropical lagoon at Zanzibar (ZNZ) and the cold-water coral degradation zone at the Porcupine Seabight (PSB), based on pooled samples per microhabitat. Families with a relative abundance >2% in at least one microhabitat (in ZNZ or PSB) are given.

It is clear that dead coral fragments are an important source of additional niches and enhance habitat heterogeneity. The different microhabitats examined in this study are important in structuring the harpacticoid communities associated with degradation products of tropical and cold-water coral reefs. Each of the microhabitats probably offers a unique set of resources and ecological interactions. The primary factors affecting composition of the associated fauna are most likely nature and structure of the primary substrate. Contrary to the surrounding sediment, the hard substrate of coral fragments obviously lacks interstitial space. The sediment assemblages are structured by differences in sediment granulometry, and this was most clear in the tropical lagoon. Furthermore, the associated faunas might experience different conditions in food and oxygen availability and different levels of hydrodynamical stress. Copepod species living phytally, epibenthically or in the water column are known to have ecological traits which differ from those in sediment-dwelling species (Marcotte, 1983; Hicks, 1985). The structurally complex dead coral fragments might provide a variety of food resources and meet the feeding requirements of both sediment and phytal taxa, which could explain their co-occurrence on the coral fragments.

Especially in the deep sea, harpacticoids are concentrated in the uppermost sediment layer because of the steep decrease in oxygen tension to which they are most sensitive (Moodley *et al.*, 1997). The well oxygenated carbonate sediments in the tropical lagoon conversely permits

harpacticoids to penetrate deeper in the sediment and this might provide more opportunities for niche segregation. Furthermore, it is likely that oxygen is not a limiting factor on the coral fragments.

Diversity

Tropical coral reefs are known as the most taxonomically diverse of all marine ecosystems. Recently, it has been stated that the diversity of *Lophelia pertusa* cold-water coral reefs might be of a similar order of magnitude to that of some shallow-water coral reefs (Rogers, 1999). Most studies of associated fauna have dealt with macro- and megafauna, and recently the associated meio- and nematofauna of dead coral substrates has been addressed (Raes & Vanreusel, 2006; Raes *et al.*, 2007). The present study aimed to assess species diversity of harpacticoid copepods associated with tropical and cold-water coral substrates and the role of microhabitat type in structuring this diversity.

In the tropical lagoon, trends in species diversity of the different microhabitats differed between both studied locations. At Makunduchi, diversity was significantly higher on coral than in gravel and upper sediment layer, whereas this was not the case at Matemwe. It was assumed that the observed differences in form and complexity of the coral fragments were the main responsible factor. Especially for phytal assemblages, the positive impact of habitat structural complexity on harpacticoid abundance and diversity has been stressed by several authors (Hicks, 1985; Gee & Warwick, 1994; Ólafsson *et al.*, 2001; Jenkins *et al.*, 2002). Greater habitable space, increased nutritional resources and reduced levels of predation or physical disturbance are thought to contribute to this relationship. Similarly, it is likely that variations in the structural complexity of coral fragments have an impact on the diversity of the associated harpacticoid assemblage, by providing increased potential for niche separation, refuge against predation and by modifying the local hydrodynamical environment with possible implications for food availability. Marcotte (1986) related complexity of the sediment substrate and the ecological grain of food resources to the diversity of benthic copepods. Larger sand particles (>300 μm) have at least one smooth facet on which the epifloral food of copepods is distributed as a coarse-grained ecological resource, while smaller sand particles have irregular surfaces on which food organisms are distributed in a fine-grained manner. The co-occurrence of two ecological grains of food resources in sediments with a mean particle diameter of 200 μm then would allow the co-existence of selective and non-selective epistrate feeders and explain high diversity (Marcotte, 1986). Dead coral fragments are subject to biological and physical erosion and it is likely that their complex microtopography consists of a variety of smooth and rough surfaces onto which food is distributed discontinuously or homogeneously. Different ecological grains of food resources on the coral fragments might allow co-existence of copepods with different feeding requirements and therefore explain high diversity. The co-occurrence of both sediment-dwellers

and phytal taxa might also be linked to the variety of food resources which could meet differences in feeding selectivity. Small sand-dwelling copepods are considered non-selective foragers which indiscriminately scrape food from the surface of small sand particles, while larger species selectively feed at centres of food growth (Marcotte, 1986). Harpacticoid assemblages of the surrounding sediment likely inhabit a structurally less complex habitat, with more uniform food resources and higher levels of predation. Further, it should be taken into account that epibenthic structure can change the water flow regime from linear to nonlinear (turbulent), with subsequent alterations of nearby sediment structure (Eckman, 1985; Nowell & Jumars, 1984; Palmer, 1986) and passive or active aggregation of harpacticoids (Thistle *et al.*, 1984; Kern & Taghon, 1986). This is the first study where coral degradation products (such as coral fragments and coral gravel) are included as a habitat for harpacticoid copepods. It is clear that by including these additional microhabitats, total species diversity of the tropical lagoon is increased substantially. As indicated by additive partitioning of diversity, these added species, however, are generally rare.

In the cold-water coral degradation zone, the harpacticoid fauna of sediment and coral fragments was characterised by high species richness and evenness, which is also the general trend in the deep sea (Coull, 1972; Thistle, 1978; Seifried, 2004). Although low species dominance, in combination with the limited sample sizes, strongly restricts comparison, it appears that both microhabitats are equally and highly diverse, and do not differ distinctly in terms of evenness. Raes & Vanreusel (2006) conversely found the nematode community of the underlying sediment significantly more diverse than on the coral fragments and attributed this to lower hydrodynamical disturbance. Apparently, species diversity of the associated harpacticoids is not strongly affected by differences in hydrodynamical stress. Due to the lack of knowledge from neighbouring Atlantic regions, it is at present difficult to assess whether regional harpacticoid diversity is increased substantially by the presence of cold-water coral fragments and glass sponge skeletons. Habitat heterogeneity of the seabed is increased and *Lophelia pertusa* reefs may therefore act as habitat islands which attract aggregations of species, including many specialist taxa that are rare in the background community.

Finally, we can assess whether harpacticoid diversity of cold-water coral degradation zones is of a similar order of magnitude to that of shallow-water tropical coral reefs. Only the sediment and coral fragments will be compared, as these microhabitat types were present in both regions. From the tropical coral substrates (sediment and coral), 1472 individuals were analysed which belonged to 112 species. Although less harpacticoid individuals (705) were identified from sediment and coral samples in the Porcupine Seabight, distinctly more species (147) were found. Rarefaction curves of pooled samples per microhabitat in the tropical lagoon at Zanzibar and the deep sea of the Porcupine Seabight indicated a similar trend (Fig. 2). Despite the large differences in sampling scale (two sites, 70 km apart along the Zanzibari coast versus six sites, within a range of 2 km in the Porcupine Seabight), it is apparent that species diversity of both microhabitats in

the tropical lagoon is lower than in the deep sea. Furthermore, assemblages in the cold-water coral degradation zone show a more even distribution, as shown by K-dominance curves (Fig. 3). These results indicate that harpacticoid species richness and evenness in cold-water coral degradation zones might be higher than in tropical coral degradation zones. This is not unexpected as the deep sea is known for its surprisingly high species diversity.

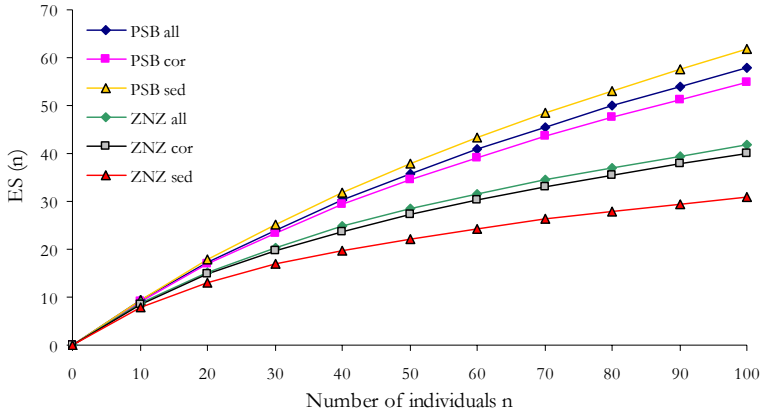

Figure 2. Rarefaction curves for pooled samples per microhabitat (sediment: sed, cor: coral) and for the combined community over both microhabitats (all), in the cold-water coral degradation zone at the Porcupine Seabight (PSB) and the tropical lagoon on Zanzibar (ZNZ).

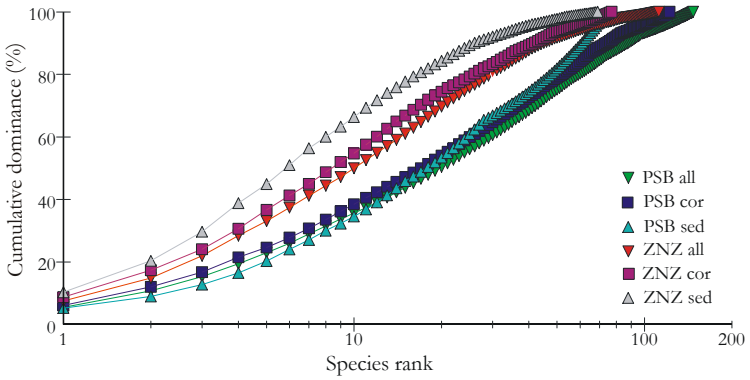

Figure 3. K-dominance curves for pooled samples per microhabitat (sediment: sed, cor: coral) and for the combined community over both microhabitats (all), in the cold-water coral degradation zone at the Porcupine Seabight (PSB) and the tropical lagoon on Zanzibar (ZNZ).

9.2. MORPHOLOGICAL ADAPTATIONS TO THE HABITAT

The Harpacticoida (one of the ten known orders of Copepoda) have successfully exploited an enormous variety of habitats. They have adopted different modes of existence which is reflected in a wide variety of body shapes and appendage modifications. The relation between habitat and body shape has been stressed by several authors (Remane, 1952; Noodt, 1971; Coull, 1977; Hicks & Coull, 1983) and morphological characteristics have even been used to predict habitat utilization and behaviour (Bell *et al.*, 1987; Thistle & Sedlacek, 2004). The present study focused on the morphological adaptations of the family Laophontidae to the different types of coral substrates that can be found in the vicinity of coral reefs. The Laophontidae are known to be highly successful in terms of species richness and number of explored habitats. They show a high degree of morphological plasticity and, therefore, are model-organisms to study the relation between habitat and morphology.

The qualitative samples of coral fragments, coral gravel and sediment from the Kenyan coast yielded 44 species of Laophontidae (see Appendix) with 28 of these new to science. Fifteen of the new species cannot be assigned unequivocally to existing genera, a fact that further highlights the evolutionary success of the Laophontidae, but also our hitherto limited knowledge of the family. Eight of the new Kenyan species were described, with three of these assigned to existing genera (*Paralaophonte* Lang, 1944 and *Tapholeon* Wells, 1967). Five species required the establishment of three new genera (*Apistophonte* Gheerardyn & Fiers, 2006, *Peltidiphonte* Gheerardyn & Fiers, 2006, *Spiniferaphonte* Gheerardyn & Fiers, 2007). It is clear that the different microhabitats, provided by the wide range of coral substrates, are occupied by laophontids with specialised morphologies. The dorsoventral flattening of the body in the new genus *Peltidiphonte* represents an adaptation to live as epifauna on the surface of dead coral fragments. This body shape, which is new to the family, should decrease the risk of being swept away by strong water currents. Furthermore, the pair of strongly prehensile first legs and maxillipeds are particularly important in seizing fine microhabitat structures that can be found in the complex microtopography of the dead coral fragments. A closely related genus, named *Propephonte* Gheerardyn & Fiers, 2006, was described from coral sand and rubble from the northern coast of Papua New Guinea. This genus is characterised by a typically fusiform prehensile, but slightly depressed, habitus, which, together with the reduced armature of the swimming legs, might indicate a more sediment-bound mode of existence. Furthermore, it was assumed that *Indolaophonte* Cottarelli, Saporito & Puccetti, 1986 and *Langia* Wells & Rao, 1987 are more derived genera within this lineage wherein setation and segmentation of the swimming legs became more reduced as an adaptation to the interstitial life-style.

The family Laophontidae displays a high degree of morphological plasticity, not only in body shape, but also in structure and shape of the appendages. An extreme example was provided by the new species *Paralaophonte harpagone* Gheerardyn, Fiers, Vincx & De Troch, 2006, of which the highly specialised maxilliped might be an adaptation to live as an associate of another

invertebrate. Reductions in setation and/or segmentation of the swimming legs are common in the family. Because as much as certain of these genera belong to different lineages, these adaptations have evolved independently several times as a result of the change in life style to the interstitial environment. Certain interstitial genera, such as the new genus *Spiniferaphonte*, are further characterised by a cylindrical body shape and the presence of strong hook-shaped processes on caudal rami and proximal segments of the antennules. It was assumed that these structures may play a role in the movement and anchoring of the animals in their interstitial habitat. Another case of convergence is apparent in the flattened caudal rami of the genera *Tapholeon* and *Asellopsis*, which is assumed to have evolved similarly in response to similar environmental conditions, being the substrate in which members of both genera are found. Both genera, however, are not closely related as evidenced by the differences in sexual dimorphism of the swimming legs. As certain adaptations to the habitat have evolved several times independently in the family, and in view of the large variety of the characteristics, it is clear that a phylogenetic analysis of the family will be difficult and should take into account the numerous cases of convergence.

It is obvious that a detailed approach of harpacticoid morphology is necessary in providing information of phylogenetic significance. The detailed characteristics of e.g. mouthparts are as yet an unexplored pool of information for phylogenetic analyses, as stated by Huys (1990). The importance of such an accurate approach was demonstrated for the new, monospecific genera *Propephonte* and *Apistophonte*. At first sight, the representatives of both genera resembled each other closely in body shape, ornamentation of the integument, chaetotaxy of the swimming legs and shape of female P5. Detailed analysis of mouthparts, structure of the proximal segment of the antennule, setation of male P5 and proportions of the endopods of the swimming legs nevertheless revealed that both species are not congeneric and inferred a close relationship of *Propephonte* with *Peltidiphonte*.

Furthermore, improved taxonomic techniques and inclusion of characters, such as body ornamentation, suggest that harpacticoid cryptic species can be distinguished based on subtle morphological characters (Huys *et al.*, 1996), thereby representing 'pseudosibling species' *sensu* Knowlton (1993). Cryptic species are known to occur among harpacticoid copepods (e.g., Ganz & Burton, 1995; Schizas *et al.*, 1999; Rocha-Olivares *et al.*, 2001), which indicates that some presumably cosmopolitan species, such as *Laophonte cornuta* Philippi, 1840, the type species of the family, could be complexes of sibling species, implying a restricted geographical distribution.

9.3. RELEVANCE AND FUTURE PERSPECTIVES

Despite their ecological importance, harpacticoid copepods have been studied rarely in the tropics. The present study of harpacticoids associated with coral substrates in a tropical lagoon provides information for understanding the functioning of the smaller size classes in these habitats. This study is innovative in that it incorporated less studied microhabitats such as dead coral fragments and coral gravel, and assessed the role of microhabitat type in structuring harpacticoid community and diversity. However, our knowledge of the relationships between coral substrates and harpacticoids is far from complete. Particularly the relationship between structural complexity of the coral fragment and harpacticoid species richness deserves attention.

At present, studies of composition, distribution and diversity of deep-sea harpacticoid communities at the species level are scarce. Nevertheless, these organisms have been labeled useful in the study of high deep-sea diversity maintenance, because of their limited dispersal capabilities, ubiquity, high abundance and high diversity (Coull, 1972; Thistle, 1998, 2001, 2003b). This study, conducted at the species level, presented the first characterisation of the harpacticoid fauna associated with cold-water coral substrates. These hard substrates represent a specific habitat in contrast to the vast expanses of the typical soft-bottom deep sea. More systematic and careful studies of neighbouring Atlantic regions, however, are necessary to assess whether regional harpacticoid diversity is increased by the structurally complex environment of *Lophelia pertusa* reefs. Moreover, more extensive sampling has to be done following specific sampling designs to get more representative counts of Harpacticoida from the deep sea.

The second part of this study focused on the morphology and taxonomy of the harpacticoid family Laophontidae. The taxonomical study of new species and genera provided new insights into the relationships within the family. Also, with the description of new species new data become available on their biogeography. It was further demonstrated that dead coral substrates provide a variety of habitats which are exploited by laophontids with specialised morphologies. In the Laophontidae, already eight of the nine harpacticoid body shapes, as classified by Coull (1977), can be found and related to the different modes of existence. Other harpacticoid families usually comprise not more than three of these body shapes (e.g. Ectinosomatidae: fusiform, vermiform, fusiform depressed; Paramesochridae: vermiform, cylindrical, fusiform depressed). The family Laophontidae shows a high degree of morphological plasticity and several hypotheses were proposed as to the functional role of the adaptations. The difficulties in unraveling the relationships within this family are mainly a consequence of this high degree of morphological plasticity.

Despite the well established monophyletic status of the Laophontidae, relationships between its 67 genera are usually not well understood. The justification for creating new genera has traditionally been based on a purely comparative approach, usually by considering a particular combination of characters as unique, rather than on phylogenetic grounds. The family has been expanding strongly since Lang's (1948) classification which included 19 genera. In 1988, Fiers provided an extensive survey and made a thorough attempt to bring order in the complete family

(Fiers, 1988). Recently, Huys & Lee (2000) subdivided the family in two subfamilies and analysed the phylogenetic relationships within the primitive subfamily of Esolinae Huys & Lee, 2000. At present, relationships within the evolutionary successful Laophontinae, comprising 95% of the known laophontid species, remain mostly unresolved and problematic. Recently, several phylogenetic analyses are being performed in the order of Harpacticoida (e.g. Huys, 1990; Martínez Arbizu & Moura, 1994; Huys & Lee, 1999; Willen 2000, 2002; Seifried, 2003; Seifried & Schminke, 2003) within groups as Laophontoidea, Cylindropsyllinae, Thalestridimorpha, Stenheliinae, 'Maxillipedasphalea' and Exanechentera. The amplification of the knowledge of Harpacticoida can therefore be based on a better foundation. The family of Laophontidae is one of the most speciose and morphologically diverse harpacticoid families and it is clear that, since its establishment one hundred years ago, this family is also in need of a thorough phylogenetic analysis. As the monophyly of several genera recognised in the past is uncertain, the analysis has to be performed at the species level. Furthermore, homoplasy appears to be a frequent phenomenon within this family, and this can only be assessed firmly after a phylogenetic analysis. The development of molecular techniques and their application in recent phylogenetic research provides a useful tool to verify if the morphology-based systematic knowledge is supported by genetic evidence. DNA sequencing can offer complementary information on phylogenetic relationships among morphologically similar taxa, as already done for many other invertebrate and particularly crustacean taxa (e.g., Abele, 1991; Abele *et al.*, 1992; Spears & Abele, 1997; Braga *et al.*, 1999; Remerie *et al.*, 2004; Huys *et al.*, 2006). The cosmopolitan family of Laophontidae is highly successful in terms of species richness and adaptive radiation, and, therefore, provides model organisms to study the history of evolution and its causes.

Esolinae Huys & Lee, 2000

Applanola hirsuta (Thompson & A. Scott, 1903)

Esola bulbifera (Norman, 1911)

Esola sp. n.

Laophontinae T. Scott, 1905 sensu Huys & Lee (2000)

Apistophonte wasiniensis Gheerardyn & Fiers, 2006

Echinolaophonte armiger (Gurney, 1927)

Echinolaophonte mirabilis (Gurney, 1927)

Echinolaophonte tropica Ummerkutty, 1970

Heterolaophonte sp. n. 1

Heterolaophonte sp. n. 2

Laophonte adduensis Sewell, 1940

Laophonte ciliata Noodt, 1964

Laophonte cornuta Philippi, 1840

Laophonte inornata A. Scott, 1902

Laophonte parvula Sars, 1908

Laophonte spinicauda (Vervoort, 1964)

Laophonte sp. n.

Loureirophonte sp. n.

Paralaophonte brevirostris (Claus, 1863)

Paralaophonte congenera (Sars, 1908)

Paralaophonte harpagone Gheerardyn, Fiers, Vincx & De Troch, 2006

Paralaophonte sp. n. 1

Paralaophonte sp. n. 2

Paralaophonte sp. n. 3

Paralaophonte sp. n. 4

Paralaophonte sp. n. 5

Peltidiphonte paracristata Gheerardyn & Fiers, 2006

Peltidiphonte ovata Gheerardyn & Fiers, 2006

Peltidiphonte rostrata Gheerardyn & Fiers, 2006

Raptolaophonte ardua Cottarelli & Forniz, 1989

Spiniferaphonte ornata Gheerardyn & Fiers, 2007

Tapholeon inconspicuus Gheerardyn & Fiers, in press

Tapholeon tenuis Gheerardyn & Fiers, in press

Wellsiphontina distincta (Wells, 1967)

Wellsiphontina striata Fiers, 1991b

Gen. n. 1 sp. n. 1

Gen. n. 1 sp. n. 2

Gen. n. 1 sp. n. 3

Gen. n. 2 sp. n. 1

Gen. n. 2 sp. n. 2

Gen. n. 3 sp. n.

Gen. n. 4 sp. n.
Gen. n. 5 sp. n.
Gen. n. 6 sp. n.
Gen. n. 7 sp. n.

Appendix. List of identified species of Laophontidae, collected from Kenya.

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