

THE UNIVERSITY OF HULL

Taxonomic, systematic, morphological and biological studies on  
*Palaemon* Weber, 1795 (Crustacea: Decapoda: Palaemonidae)

being a Thesis submitted for the Degree of  
PhD in Biological Sciences

in the University of Hull

by

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December 2012







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*for my wife and children*





## Acknowledgements

This section of the thesis is perhaps the most difficult section to write as gratitude can not be justified by citing endless references or applying any statistical tests. Despite this I am well aware that this is likely to be the most read part of the thesis and many people will probably get no further through the thesis. For any people I have omitted, I am truly sorry; this is not a reflection on you or the value of your contributions. Likewise, the order in which people are acknowledged does not reflect the value of their contribution; all contributions have been equally valuable and all have helped me get to this point.

Unicomarine (and subsequently Thomson Unicomarine) are thanked for financial support, providing time and resources to enable the completion of these studies.

All my work colleagues, both past and present, are thanked for advice, friendship, help and shouldering the extra burden of work to allow me to concentrate on my studies. Most of all they are thanked for tolerating my shrimp obsession and the occasional stench of years-old, sometimes poorly preserved pots of shrimps. Unfortunately for them, whilst the thesis is complete, the obsession continues. Special thanks are due to Tim, Lydia and Charlotte who have borne the brunt of this responsibility.

Lisa Conyers, Laura Goulding, Kate Pocklington and Louisa Wood are thanked for their help and conversation during various visits to OUMNH. Dirk Platvoet (ZMA) is thanked for his hospitality during a visit to the ZMA and for providing one of the best pieces of advice I have received. Miranda Lowe and Paul Clark (NHM) are thanked for allowing me access to their collection and for support during visits to their museum. Fiona Ware (NMS), Karen van Dorp and Jacques Smit (Naturalis), Regis Cleva (MNHN), Stephen Keable (AM), Gavin Dally (NTM), Tin-Yam Chan (NTOU), Karen Reed (USNM), Eduardo Spivak, Christoph Lejeusne, Melanie Béguer and Michel Girardin amongst others have provided valuable specimens for study. Charles Fransen (Naturalis) is also acknowledged for providing specimens, advice, information and insightful conversations.

Thanks to my fellow students at the STRI Training in Tropical Taxonomy: Short Course in Shrimp Taxonomy (Caridea, Dendrobranchiata and Stenopodidea),

Betel Martínez-Guerrero, Juan Felipe Lazarus-Agudelo, Jure Jugovic, Laura Anderson, Nuno Simões, Leslie Harris, Carolina Tavares, Patricio Hernáez, Javier Luque, Nicola Dobson, Lucas Torati and Tim Page; I learned from you all. In particular Rachel Collin secured the funding and helped with the organisation of this course.

Tim Page is thanked for his patience, advice, help, being the only person able to explain genetic theory to me such that I now have some understanding and for showing me how presentations can and should look.

Cédric d’Udekem d’Acoz and Arthur Anker are gratefully acknowledged for numerous stimulating conversations, supplying difficult to obtain literature, friendship and advice.

To my supervisors Magnus Johnson (University of Hull) and Sammy De Grave (Oxford University Museum of Natural History) I owe a huge debt of gratitude. Their continuing advice, patience, guidance, support, encouragement and, above all, friendship has made this study a possibility. Their own passion for the subject has been a huge motivational force.

Above all else, the support and love of my family, both during the completion of these studies and elsewhere in my life, has been vital to the realisation of this work. To my parents, thank you for your love, encouragement, advice and the sacrifices made throughout my life and for believing in me. Thanks are also due to my brother and sisters who have similarly provided love and support. To my children, Adam and Alice, thank you for making me smile and laugh and for understanding why I haven’t always been able to play. Finally, without the love and support of my wife, Catherine, this study simply wouldn’t have been possible. Throughout the many ups and downs of this work she has stood beside me and encouraged me. Many days, evenings and weekends she has become a ‘shrimp-widow’ as I have buried my head in the books or locked myself away with a microscope and some shrimps, yet she has never once complained or protested. One day I hope I can reciprocate but until such time I can only express my heartfelt thanks.





## General Abstract

*Palaemon* is a large genus of marine, brackish and freshwater shrimps and are amongst the most familiar shrimps to scientists and amateur naturalists. Despite being familiar and widely reported they remain understudied. A series of studies was conceived to address some of the outstanding questions on the taxonomy, systematics, functional morphology and invasive biology of *Palaemon* and related genera.

As previous studies have revealed that there is a lack of stable morphological characters to define both species and the genus *Palaemon* itself traditional taxonomic studies were conducted to highlight the potential of novel characters to delineate species and genera within the subfamily Palaemoninae. Previous phylogenetic work, both morphological and molecular, has also suggested that the genus probably does not represent a monophyletic lineage. The previous molecular phylogenetic studies were expanded on to give a phylogeny of the subfamily Palaemoninae based on the genes 16SrRNA and Histone (H3), representing the largest dataset to date on this subfamily. As the structure and morphology of an animal may also be heavily influenced by its function, an investigation into the structure of the mandible, a feature that has been attributed phylogenetic significance, was conducted via SEM to test the theory that its structure is actually a result of its function rather than its evolutionary relationships. Two previously reported forms of *P. longirostris* from brackish waters in Atlantic Europe were subjected to a geometric morphometric analysis to investigate alleged differences in carapace and rostrum shape. Two different studies were instigated to investigate the invasive species *Palaemon macrodactylus*. The first of these scrutinised and synthesised available data and presented hypotheses on modes of spread, patterns of spread, potential impacts, factors favouring its introduction and made predictions of areas at risk of future invasion. The second study investigated the potential impact of the introduction of *P. macrodactylus* on the native *P. longirostris* in the River Thames by analysing dietary overlap from stomach content analysis.

As a result of the taxonomic studies two new species of *Palaemon* were described from the tropical eastern Atlantic: *Palaemon powelli* and *P. vicinus* and a further, poorly known species was redescribed. A new genus, *Rhopalaemon*, was also erected to accommodate the rather aberrant, Indian species *Leander belindae* which had previously been included in *Palaemon* for many years. Several characters that

had not previously been used or had not been attributed much significance were used in the definition of these taxa. A taxonomic guide to the marine Palaemoninae fauna of Taiwan was created reporting thirteen species belonging to seven genera. One of these species, *P. serrifer* occurs in two distinct morphotypes in Taiwan, one of which is suspected to be a new species.

The molecular phylogenetic study indicated that *Palaemon* as presently defined is not a monophyletic genus with the genera *Exopalaemon*, *Coutierella* and *Palaemonetes* likely being synonyms of *Palaemon*. *Palaemon concinnus*, *P. pandaliformis* and *P. gracilis* do not form a clade with other *Palaemon* and should be removed from the genus. As well as the systematic implications, the molecular study also revealed that freshwater species do not form a clade with one another but rather are more closely related to geographically proximate species suggesting that they arise from multiple invasions of freshwaters rather than a single invasion and subsequent radiation.

The functional morphology of palaemonoid mandibles was investigated via scanning electron microscope. The presence of cuticular structures was noted on most mandibles with five distinct types being recognised. Each type of cuticular structure is presumed to have a different function. The results indicated that only a weak phylogenetic signal is conveyed by the structure of the mandible but that its structure is influenced by the food sources ingested. Those species that consume harder prey items had mandibles designed for grinding with presumed mechanosensory cuticular structures whilst those consuming soft-bodied prey did not possess cuticular structures. Feeding on particulate or mucous diets has resulted in highly modified mandibles. In order to try to categorise the variety of morphological form of the mandible and of the cuticular structures a new classification system was developed.

The two reported morphological forms of *Palaemon longirostris* with a divide in the southern Bay of Biscay were supported by the geometric morphometric analysis. The forms chiefly differed in the form of the rostrum with the southern form having a more elongate and upwardly directed rostrum than the northern form. However, no biological grounding was found to support the morphological differences observed.

The global distribution of *Palaemon macrodactylus* appears to have originated through a combination of at least three primary introductions from Asia and three secondary introductions. The factors that have lead to *P. macrodactylus* being so

widely transported are still unclear as many of its life history traits and environmental tolerances are similar to other species of *Palaemon* that have not invaded. It is suggested that its advantage may lie in the tolerances of its larvae. The competitive interactions of the species in newly invaded regions are poorly known but the data obtained here suggest strong trophic overlap with *P. longirostris* in the Thames during the winter but less so in the summer. This seasonal aspect to the overlap in the diet may also provide differing opportunities for successful invasion by *P. macrodactylus* with greater chance of success in the summer when competition for food is lower. The diet of *P. macrodactylus* in the Thames is slightly different to that reported for other regions to which it has been introduced being dominated by amphipods rather than mysids. If food becomes a limiting factor, particularly in summer, then the competition between *P. macrodactylus* and *P. longirostris* may increase leading to potentially adverse effects on the latter species.

This study has increased the number of species of *Palaemon* from 39 to 41 through the description of two new species and removed a further species to a new monotypic genus, *Rhopalaemon*. However, the molecular analysis indicates that the true number of species that belong in the genus is approximately double this number and that further species should be removed to other, new genera. It has demonstrated that the freshwater species have independently invaded freshwater and that species of the genus are prone to human-mediated introductions. A new system for the classification of caridean mandibles and cuticular structures is proposed and their form has been linked to diet and feeding mode.





## General Introduction

The shrimp genus *Palaemon* Weber, 1795 consists of medium to large sized shrimps that are widely distributed in shallow tropical, warm and temperate waters throughout the world and are found in marine, brackish and freshwaters. They are often abundant where they occur and are usually reasonably easy to sample using dip-nets, baited traps or beam trawls. Many species can be found in easily accessible habitats such as rock pools or shallow embayments and as such they are familiar to biologists and amateur naturalists. The genus *Palaemon* currently contains 41 known species (De Grave & Fransen, 2011) although the status of some of these may require evaluation. Of the 22 recognised genera in the subfamily Palaemoninae it is second only in the number of constituent species to the genus *Macrobrachium* Spence Bate, 1868, which contains in excess of 242 species (De Grave & Fransen, 2011). Six fossil species from the Upper Cretaceous, Lower Cretaceous and Oligocene have also been tentatively referred to the genus (Bravi et al., 1999; Garassino & Bravi, 2003; De Grave et al., 2009).

Of the currently known species of *Palaemon*, 23 are found in marine waters, five are found in freshwater, 11 in brackish/estuarine conditions and two have been reported from all three environments. Many of the marine species and some of the freshwater species will also occasionally occur estuaries with some typically marine species being able to tolerate water of 1 PSU for extended periods (Sanz, 1982). The freshwater species typically occur in slow moving rivers and streams and are often associated with marginal vegetation; marine species are typically found in pools, associated with seaweeds or hidden amongst boulders. The Mediterranean and warm Atlantic species *P. xiphias* is found exclusively amongst seagrass (*Posidonia* spp.), where other species may also occur. All the marine species occur in shallow water with a probable depth limit of around 50 m. Several extensive works have been conducted describing regional *Palaemon* faunas, for example by Holthuis (1952) for North and South America, Walker and Poore (2003) for Australia, Kubo (1942) for Japan and Li et al. (2007) for China. However, despite these works, many regional faunas remain poorly known and no up to date synopses or identification guides exist. The number of species known in each region, including any non-native and freshwater species, is shown in Figure 1.

Most species of *Palaemon* are common, widespread and often abundant where they occur although some species such as *P. peruanus* and *P. yamashitai* are known only from single records and others have very restricted distributions or habitat preferences suggesting they are at risk from human activities. Those assessed as part of a recent assessment for the IUCN Red List of Threatened Species were listed in the ‘least concern’ category (S. De Grave, pers. comm.) but the criteria for this assessment meant few species qualified for assessment. The conservation status of *P. longirostris* was reviewed by Chadd & Extence (2004) who considered it to have conservation value due to its patchy distribution and restricted habitat. The same may be true for many of the other species occurring elsewhere in the world.



**Figure 1.** The number of known species of *Palaemon* occurring in each biogeographic region. Number includes non-native and freshwater species.

### *Life History of Palaemon*

*Palaemon serratus* is the largest species in the genus attaining a length of up to 12 cm (Forster, 1951a). Female *Palaemon* are larger than and grow at a faster rate than males (Guerao et al., 1994). In the temperate species at least, growth is not continuous throughout life and ceases in periods of lower temperature (Berglund, 1981; Omori & Chida, 1988). Life spans of around three years are reported for *P. serratus* and *P. elegans* (Forster, 1951a, b), 14-17 months for *P. xiphias* (Guerao et

al., 1994), 12-13 months for *P. paucidens* (Kim et al., 2008) and two years for *P. macrodactylus* (Omori & Chida, 1988). Breeding tends to be seasonal in the temperate species (Forster, 1951a, b; Smaldon et al., 1993; Kim & Hong, 2004; Kim, 2008; Bilgin et al., 2006, 2009a, 2009b), although there may be more than one brood per season. There is a lack of published data on the reproductive biology of the tropical species of *Palaemon* (Corey & Reid, 1991), but it may be expected that the breeding season would be extended or, perhaps, continuous in these species (Sastry, 1983; Bauer, 1989; pers. obs.).

*Palaemon* have a planktonic larval phase and with the larval development of several of the species having been studied (Little, 1969; Fincham, 1977, 1979, 1983, 1985; Fincham & Figueras, 1986; Shy & Yu, 1987; Gamba, 1998; Knowlton & Vargo, 2004; Shy et al., 2005). Most of the species have around seven larval stages, although occasionally up to ten may be obtained (Gamba, 1998). This may enable the larvae to delay metamorphosis until favourable conditions are encountered. Marine species conduct their entire life cycle in fully saline waters but some of the freshwater species are apparently reliant on some salt water input for their development. In nature, larvae of the freshwater species *P. pandaliformis* are believed to develop in brackish water (Anger & Moreia, 1998), however, Gamba (1998) successfully reared the larvae in freshwater, indicating this may be possible in nature. Conversely the larvae of the marine species *P. northropi* are only able to survive for a few hours in freshwater (Anger & Moreia, 1998).

#### *Diet of Palaemon*

Studies on the diet of *Palaemon* have demonstrated a variety of feeding strategies and indicated that they may be a vital link between the lower trophic levels and primary producers and higher trophic levels. Many are omnivorous with debris, algae, molluscs and crustaceans forming a large proportion of the diet (e.g. *P. serratus* and *P. elegans* – see Forster, 1951a, 1951b; Janas & Barańska, 2008) whilst others are predominately carnivorous (e.g. *P. xiphias* and *P. macrodactylus* – see Sitts & Knight, 1979; Siegfried, 1982; Guerao, 1995). Both scavenging and predation have been recorded as feeding strategies (Forster, 1951a) and there is also evidence of cannibalism when kept in crowded laboratory conditions (Newman, 1963) although it is unknown whether this occurs in natural conditions. Regional differences in diet

composition, reflecting local differences in food availability, have also been reported (Janas & Barańska, 2008).

### *Commercial Importance of Palaemon*

Many species of *Palaemon* are too small to be of value for human consumption but some of the larger species support commercial fisheries. Some of the smaller species, however, are used for bait (leading to some species being commonly known as bait prawns), support small subsistence fisheries or occur as by-catch in fisheries for other species. Holthuis (1980) lists fifteen species of *Palaemon* as having interest to fisheries. Subsequently, Nguyễn (2000) indicated that *P. sewelli* may also have commercial value as feed for groupers and ducks. Of the nine species described since Holthuis (1980) only *P. powelli* has been described as having any commercial value, occurring as by-catch to the fishery for *Nematopalaemon hastatus* (Aurivillius, 1898) in the Niger Delta, West Africa (see Ashelby & De Grave, 2009). The most important commercial fisheries are based on the European species. *Palaemon serratus* is the largest species of the genus, and possibly the most commercially valuable. In Ireland it is fished for using baited traps and annual landings may reach 548 tonnes (Fahy et al., 2006). On the French Atlantic coast annual landings are approximately 700 tonnes (Holthuis, 1980). The species is also commonly fished for in Spain where it attracts high prices (pers. obs.) with prices rising further in winter when they become more difficult to catch (Ramón Muiño, pers. com.). Berried (egg carrying) females fetch the highest prices and are the target of the fishery (Fahy et al., 2006). Jensen (1958) described the Danish fishery for *P. adspersus* where annual catch ranges between 100 and 300 tonnes. *Palaemon longirostris* is commercially fished in south-west France (Sorbe, 1983) although Hamond (1971) described the species as lacking in flavour and rather muddy to the taste.

As well as this direct commercial value, *Palaemon* spp. form an essential part of the food web in many ecosystems and may therefore be of indirect commercial importance as food for commercial fish. Cabral & Costa (2001) reported *Palaemon* spp. in the diet of juvenile sea bass (*Dicentrarchus labrax* L., 1758) and Gruszka & Wicaszek (2011) reported that *P. elegans* is important in the diet of cod (*Gadus morhua* L., 1758). It is probable that other species also occur in the diet of

commercial fish species. Several species of the closely related genera *Macrobrachium* and *Palaemonetes* are becoming increasingly common in the aquarium trade and it is possible that some *Palaemon* species may eventually appear in the trade.

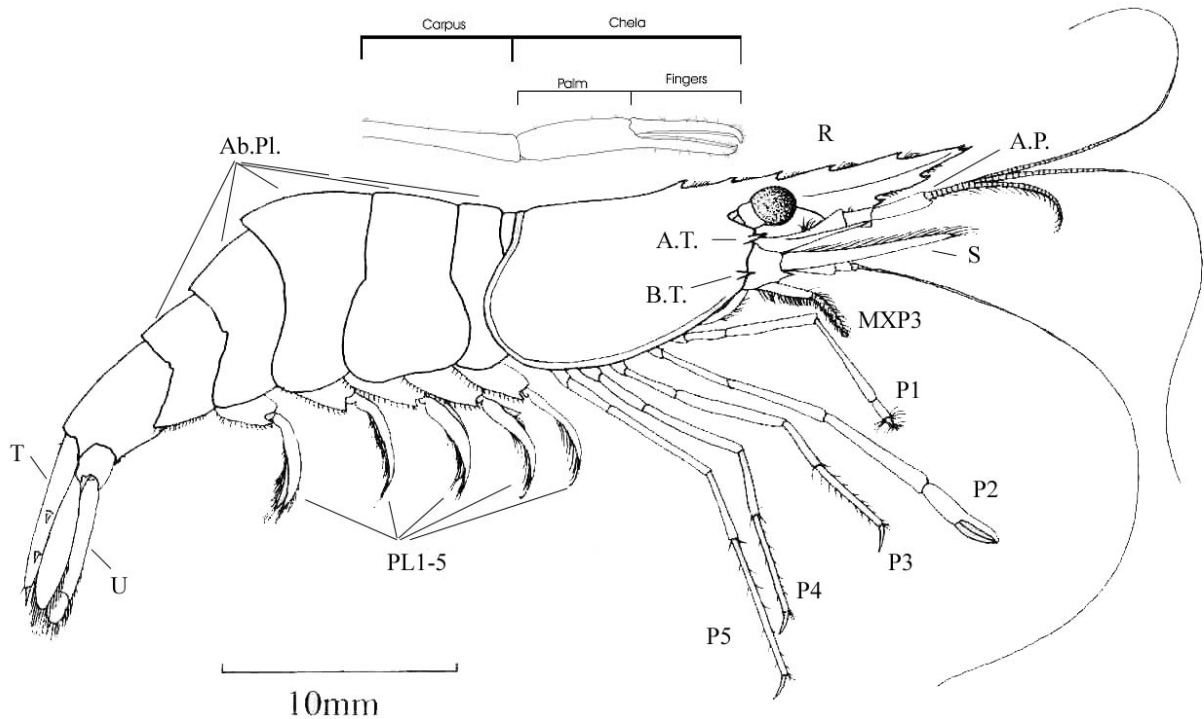
#### *Human-mediated Spread of Palaemon*

To date, four species of *Palaemon* have been recorded as non-native in various areas and potentially having adverse effects on native communities. Both *Palaemon adspersus* and *P. elegans* have been recorded from the Caspian Sea and Aral Sea; their introduction to these areas in the early 1930s is believed to be coincidental with the introduction of mullet (Zenkevich, 1963). Holthuis and Hassan (1975) report *Palaemon elegans* from Iraq and it has also recently been reported as an alien in the Baltic Sea (Janas et al., 2004). Most recently the presence of *P. elegans* in the Sound of Salem, Massachusetts has been noted (J. Carlton, pers. comm.). Sezgin et al. (2007) report the occurrence of a single specimen of *P. longirostris* in the southern Black Sea, but discrepancies in its ecology leave this record in doubt. However, none of these species has achieved the global spread of *P. macrodactylus*. So successful has this species been at invading regions outside of its natural range it has earned the common name migrant prawn. From its native range in Japan, Korea and China it has spread to San Francisco Bay (Newman, 1963), Australia (Buckworth, 1979), Argentina (Spivak et al., 2006), European Atlantic Coasts (Cuesta et al., 2004; Ashelby et al., 2004; d'Udekem d'Acoz et al., 2005; Béguer et al., 2007; González-Ortegón et al., 2007; Chícharo et al., 2009), Black Sea (Micu & Niță, 2009; Raykov et al., 2010) and, most recently, the eastern U.S.A. (Warkentine & Rachlin, 2010). Most of these reports cite ballast water as the most likely vector for its spread and the effects of its introduction on native fauna are poorly understood.

#### *Morphology of Palaemon*

The general structure of a *Palaemon* is shown in Figure 2, using *P. adspersus* as a model. The body comprises a cephalothorax and an abdomen (or pleon). The cephalothorax is covered by a carapace which, in turn, possesses an anteriorly directed projection, the rostrum. The rostrum is laterally compressed and is armed on

both the dorsal and ventral margin with teeth. The carapace possesses two teeth, a branchiostegal tooth and an antennal tooth, on or close to its anterior margin and a



**Figure 2.** *Palaemon adspersus* Rathke, 1837. Ab.Pl. – abdominal pleurae; A.P. – antennular peduncle; A.T. – antennal tooth; B.T. – branchiostegal tooth; MXP3 – third maxilliped; P1, P2, P3, P4, P5 – pereopods 1-5; PL1-5 – pleopods 1-5; R. – rostrum; S. – scaphocerite; T. – telson; U. – uropods. After Smaldon et al. (1993). Pereiopod 2 Carpus and Chela inset. Not to scale.

branchiostegal groove that runs posteriorly from the anterior margin. There are five pairs of pereopods (‘walking legs’) attached to the thorax. Each pereopod comprises seven segments: the coxa, basis, ischium, merus, carpus, propodus and dactylus. The first two pairs of pereopods possess chelae (‘claws’) and are used in manipulation of food and cleaning; the remaining pereopods are unmodified and end in a simple dactylus. The abdomen possesses five pairs of pleopods (‘swimming legs’) each comprising an endopod and an exopod. The endopod of the second to fifth pleopods

has an appendix interna which link together to aid synchronisation during swimming. The second pleopod of males also possesses an appendix masculina which is used during copulation and sperm transfer. The sixth abdominal segment bears a pair of uropods and a telson, which together are sometimes termed the ‘tail (or caudal) fan’.

### *Taxonomy of Palaemon*

*Palaemon* are notoriously difficult to identify, even on local scales, but on a worldwide basis this situation is amplified. A *Palaemon* specimen without any form of locality data may prove impossible to identify. This is due, in part, to their largely conservative morphology (Figure 2) and a lack of stable diagnostic characters for the species. Species identification has typically relied on rostral features (e.g. shape and dentition, number of rostral teeth situated behind the orbit), proportion of the segments of the second pereiopod — particularly the ratio of the fingers/palm and the chela to the carpus (Figure 2, inset), the ratio between the fused and free portions of the shorter ramus of the antennule, and the number of segments of the mandible palp.

For many species the shape of the rostrum has been used as a diagnostic character. However, as this is subjective the use of shape as a definitive character will likely lead to misidentifications. Whilst most of these characters undoubtedly have importance in the identification of *Palaemon*, some are now known to exhibit considerable intraspecific variation and reliance on these characters in being the sole defining characters of a species has led to many species having long and complex synonymies. There is therefore a pressing need for the establishment of stable, species specific characters to aid the definition and recognition of *Palaemon* species globally.

### *Systematics of Palaemon*

*Palaemon* is a member of the one of the largest caridean shrimp families, the Palaemonidae, and, in turn, one of the largest superfamilies, the Palaemonoidea. The Palaemonidae is the only shrimp family to contain currently recognised subfamilies: the Palaemoninae and the Pontoniinae (De Grave & Fransen, 2011). The Pontoniinae is restricted to tropical and, to a lesser extent, temperate marine waters. Many pontoniids are commensal and this has led to high diversity and a wide variety in

morphology, however many of the free living species share a similar gross morphology with members of the Palaemoninae and it is difficult to separate the family on the basis of adult morphology alone. Historically, a number of other subfamilies have been recognised in the Palaemonidae but, with the exception of the Pontoniinae, these have all been elevated to family level within the superfamily Palaemonoidea (see De Grave, 2007 for discussion). A recent study (Bracken et al., 2009) has also suggested that the family Palaemonidae as presently conceived is not monophyletic<sup>1</sup>. In addition, the family Kakaducarididae Bruce, 1993 falls within the Palaemonidae genetically (Page et al, 2008; Bracken et al., 2009) and is likely to be formally synonymised in the future.

Delineation between the 21 recognised genera of the Palaemoninae is becoming increasingly problematic due to the paucity of useful diagnostic characters. Generic placement is generally based on the combination of presence/absence of a hepatic or branchiostegal tooth, a branchiostegal groove, a grooming brush on the fifth pereopod, an appendix interna on the first pleopod of males, a mandible palp and a tooth on the fourth thoracic sternite. Based on these characters, within the subfamily, *Palaemon* falls within a group of genera that includes *Palaemonetes* and *Coutierella* and to a lesser extent *Macrobrachium*, *Leander* Desmarest, 1849 and *Pseudopalaemon*.

Holthuis (1950) split the genus *Palaemon* into four subgenera: *Palaemon* (*Nematopalaemon*), *P.* (*Exopalaemon*), *P.* (*Palaemon*) and *P.* (*Palaeander*). *Nematopalaemon* is defined by having an elevated basal crest to the rostrum and exceptionally long slender dactyli to the pereopods. *Exopalaemon* is defined by having a strong basal crest to the rostrum as well as lacking a tooth on the fourth thoracic sternite. *Palaeander* contained those species believed to have a two segmented mandible palp whilst *Palaemon* contained those species that had a three segmented mandible palp. At that time Holthuis (1950) believed that the number of segments of the mandible palp was a stable character and of high importance in the taxonomy of the group. However, several later studies (Fujino & Miyake, 1968; Chace, 1972; Tirmizi & Kazmi, 1984) showed intraspecific variability in this character calling into question its reliability at a generic or subgeneric level. Chace & Bruce (1993) later elevated *Nematopalaemon* and *Exopalaemon* to full generic rank

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<sup>1</sup> Monophyletic – group containing all the descent of a common ancestor. Paraphyletic (or polyphyletic) groups contain only part of the descent of a common ancestor.



but did not recognise *Palaeander* due to the inherent variability of the mandible palp in some species.

A morphological phylogenetic study of Pereira (1997) as well as genetic evidence provided by Murphy & Austin (2004, 2005), Liu et al. (2007), Wowor et al. (2009) has indicated that *Palaemon*, as presently conceived, is not a monophyletic genus. Under the Linnaean binomial system currently used in species classification the concept of a monophyletic genus is important. Monophyly implies common descent. If a genus can be regarded as monophyletic then knowing the genus that a species belongs to enables inferences to be made about that organism and its relationships to other species to be investigated. The genetic studies mentioned have only included *Palaemon* as an outgroup in the analysis whilst concentrating on *Macrobrachium* and therefore the data provided by these studies is limited to a small number of species and can be regarded as indicative only. Pereira's (1997) study included the majority of species known up to that date and indicated that *Palaemon* and *Palaemonetes* are paraphyletic<sup>2</sup>, with the two genera spread into several smaller monophyletic groups. The systematics of both the family and the genus are therefore far from resolved and changes in the classification of the group are likely.

#### *Aims of this Study*

This study set out with the aim of resolving some of the outstanding problems with *Palaemon*. Specifically, targeted studies on the taxonomy and morphology of *Palaemon* were conceived to assess novel, potentially informative morphological characters for their taxonomic, species recognition, functionality and phylogenetic significance as well as the factors that drive the evolution of these characters. Systematic studies were designed to assess the position of *Palaemon* in relation to the other genera of the Palaemoninae. Studies were also conceived to assess the spread and potential impact on native species and ecosystems of *Palaemon macrodactylus*, recently introduced to many regions outside of its native range.

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<sup>2</sup> See footnote 1.

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## Chapter 1: Taxonomy of *Palaemon*

1. A new species of *Palaemon* (Crustacea, Decapoda, Palaemonidae) from West Africa, with a re-description of *Palaemon maculatus* (Thallwitz, 1892).

[Published in: *Zootaxa* 2085: 27-44 (2009)]

2. *Palaemon vicinus* sp. nov., (Crustacea: Decapoda: Palaemonidae) a new species of caridean shrimp from the tropical eastern Atlantic.

[Published in: *Zoologische Mededelingen Leiden* 83(27): 825-839 (2009)].

3. A new genus of palaemonid shrimp (Crustacea: Decapoda: Palaemonidae) to accommodate *Leander belindae* Kemp, 1925, with a redescription of the species.

[Published in: De Grave, S. & Fransen, C.H.J.M. (eds.). 2010. Contributions to shrimp taxonomy. *Zootaxa* 2372: 1–414].

4. Marine and estuarine shrimp fauna of Taiwan (Crustacea: Decapoda):  
Subfamily Palaemoninae.

[In press: Chan, T.-Y. (ed) Crustacean fauna of Taiwan: Shallow water shrimps, Volume I — Caridea, Dendrobranchiata, Stenopodidea. Keelung, Taiwan: National Taiwan Ocean University]



**A new species of *Palaemon* (Crustacea, Decapoda, Palaemonidae) from West Africa, with a re-description of *Palaemon maculatus* (Thallwitz, 1892)**

**Abstract**

A new species of *Palaemon*, *P. powelli* sp. nov., is described from tropical West Africa. The new species is characterised by the shape and proportions of its chelae, the shape of the rostrum, spacing between dorsal rostral teeth and a poorly developed grooming brush on the fifth pereopod. *Palaemon maculatus* (Thallwitz, 1892) is redescribed and can be separated from other eastern Atlantic members of the genus by the form of the rostrum, the proportions of the segments of pereopod 2 and the large number of rows of setae in the grooming brush on the fifth pereopod.

**Introduction**

The known tropical West African marine and brackish water palaemonine fauna currently consists of 7 species in 5 genera (Holthuis, 1951), with an undescribed species being mentioned as long ago as 1983 (Powell, 1983). Several freshwater species of *Macrobrachium* Bate, 1868 also occur in the region, some of which could perhaps be found in oligohaline waters. Three species of *Palaemon* Weber, 1795 are reported from the area, one of which is currently considered endemic to the region. The other two species recorded from West Africa, *Palaemon elegans* Rathke, 1837 and *P. serratus* (Pennant, 1777), are assumed to have large geographic ranges in the eastern Atlantic. *Palaemon elegans* is reported from south-western Norway to southern Namibia, including the Mediterranean and the Black Sea; whilst *P. serratus* occurs from Denmark southwards to Cape Blanco (Western Sahara) (Holthuis, 1951). The only West African endemic species so far recorded, *Palaemon maculatus* (Thallwitz, 1892), occurs from Liberia (Rathbun, 1900; Johnston, 1906) southwards to southern Angola (Balss, 1916).

In reports on the decapod crustaceans of the Niger Delta, Powell (1983; 1985) mentions an undescribed species of *Palaemon* occurring in the region based upon extensive samples in the years 1975-1980. In the earlier paper (Powell, 1983), a brief diagnosis of the species was given, along with the vernacular name ‘Blackegg prawn’

and the suggestion it should be referred to as *Palaemon* species A, of Powell, 1982 until a description becomes available. The intent to produce such a description was announced by (Powell, 1985), but did not appear by the time of his death in 1998 and it is unlikely to appear posthumously. Based on a series of specimens deposited in Naturalis (Leiden) and in the Natural History Museum (London) the species is described here, as part of an ongoing revision of *Palaemon*, and dedicated to its discoverer, C.B. Powell. As no full description of the other endemic West African *Palaemon* species, *P. maculatus* exists, the opportunity is taken to rectify this and it is redescribed herein.

### **Material and Methods**

All specimens were examined with the aid of microscopes. Measurements (+/- 0.1 mm) were made with an optical micrometer fitted to the eyepiece. Post orbital carapace length was used as the standard measurement for whole animals and was measured in a straight line from the posterior margin of the orbit to the posterior margin of the carapace. For large structures and appendages examination took place under a Nikon SMZ-U fitted with x15 eyepieces and a working range of 0.75-7.5 x magnification. Finer structures were examined using a Nikon Labophot compound microscope with fitted with x10 to x100 objectives. To improve contrast and to aid examination of less easily discerned features, specimens were occasionally stained with Chlorazol Black.

Specimens were dissected under the microscope with appendages removed in sequence from posterior to anterior. Removed appendages were placed separately into labelled Petri dishes. For smaller appendages, temporary slides were made with structures mounted in either 70% ethanol or lactophenol. Typically, appendages were only removed from one side of the animal.

Whole animal and large structure drawings were prepared using a Camera Lucida attached to a Wild M5 microscope. For smaller structures, such as mouthparts, drawings were prepared using a Camera Lucida attached to a Leica DMLB. The magnification employed for each drawing was noted. Where necessary, the pencil drawings were reduced from their original size to fit on a single A4 sheet of paper using a photocopier. A record was made of the percentage reduction for later scaling of the drawings. Once at A4 size, copies of the drawings were made onto

drawing film using Rotring pens and a drawing board. The inked drawings were digitised using a flatbed scanner, scanned as black and white images at a resolution of 600dpi and saved as LZW compressed TIFF files. The digital images were opened in Adobe® Photoshop® to correct any minor imperfections. Finally, the images were imported to CorelDRAW® where they were manipulated and arranged as a plate with other related images. Scale bars were applied taking into account the original magnification and the subsequent reductions at the photocopying and final manipulation stages. Where possible reductions were standardised to minimise the number of scale bars needed.

The following abbreviations are used in the text: pocl. (post orbital carapace length), NHM (Natural History Museum, London), OUMNH-ZC (Oxford University Museum of Natural History Zoological Collection), RMNH (Rijksmuseum van Natuurlijke Historie (= Nationaal Natuurhistorisch Museum, Naturalis, Leiden), USNM (United States National Museum of Natural History, Smithsonian Institution, Washington).

### Systematics

Family Palaemonidae Rafinesque, 1815

Subfamily Palaemoninae Rafinesque, 1815

*Palaemon* Weber, 1795

***Palaemon maculatus* (Thallwitz, 1892)**

### Figures 1-2

*Leander maculatus* – Thallwitz, 1892: 19-20, 49, fig. 4. – Rankin, 1898: 246. – De Man, 1923: 3. – Kemp, 1925: 290. – De Man, 1925: 36-38, figs. 8a-d. – Barnard, 1950: 782-783. – Dartevelle, 1950: 33.

*Palaemon edwardsii* (nec *Palaemon Edwardsii* Heller, 1863). – Rathbun, 1900: 314.

*Leander edwardsii* (nec *Palaemon Edwardsii* Heller, 1863). – Johnston, 1906: 862. – Balss, 1916: 26-27.

*Palaemon* (*Leander*) *Edwardsii* (nec *Palaemon Edwardsii* Heller, 1863). – Lenz, 1910: 126

*Palaemon maculatus*. – Rathbun, 1900: 314-315. – Schmitt, 1926: 25-27, fig. 65. – Holthuis, 1951: 140-142. – Holthuis, 1952: 56-57. – Darteville, 1951: 1021. – Ribeiro, 1970: 9, 12, 59. – Powell, 1983: 274, fig. 16. – Powell, 1985: 235. – Jayachandran, 2001: 213.

*Palaemon (Palaeander) maculatus*. – Holthuis, 1950: 8, 55. – Monod, 1954: 111, 114, 127-128, 136. – Kensley, 1972: 44, fig. 19o. – Lefevre, 1970: 2.

? *Leander adpersus*. – Sharp, 1893: 119.

**Material examined.** 2 ♂♂, pochl. 4.8, 5.0 mm; 10 ovigerous ♀♀, pochl. 5.0 – 6.8 mm; 4 ♀♀, pochl. 5.5 – 7.0 mm; Nigeria, Bonny River, Hughes Channel, right bank; 04°37'00''N 07°07'25''E; 31.05.1980; leg. C.B. Powell; USNM 181904.

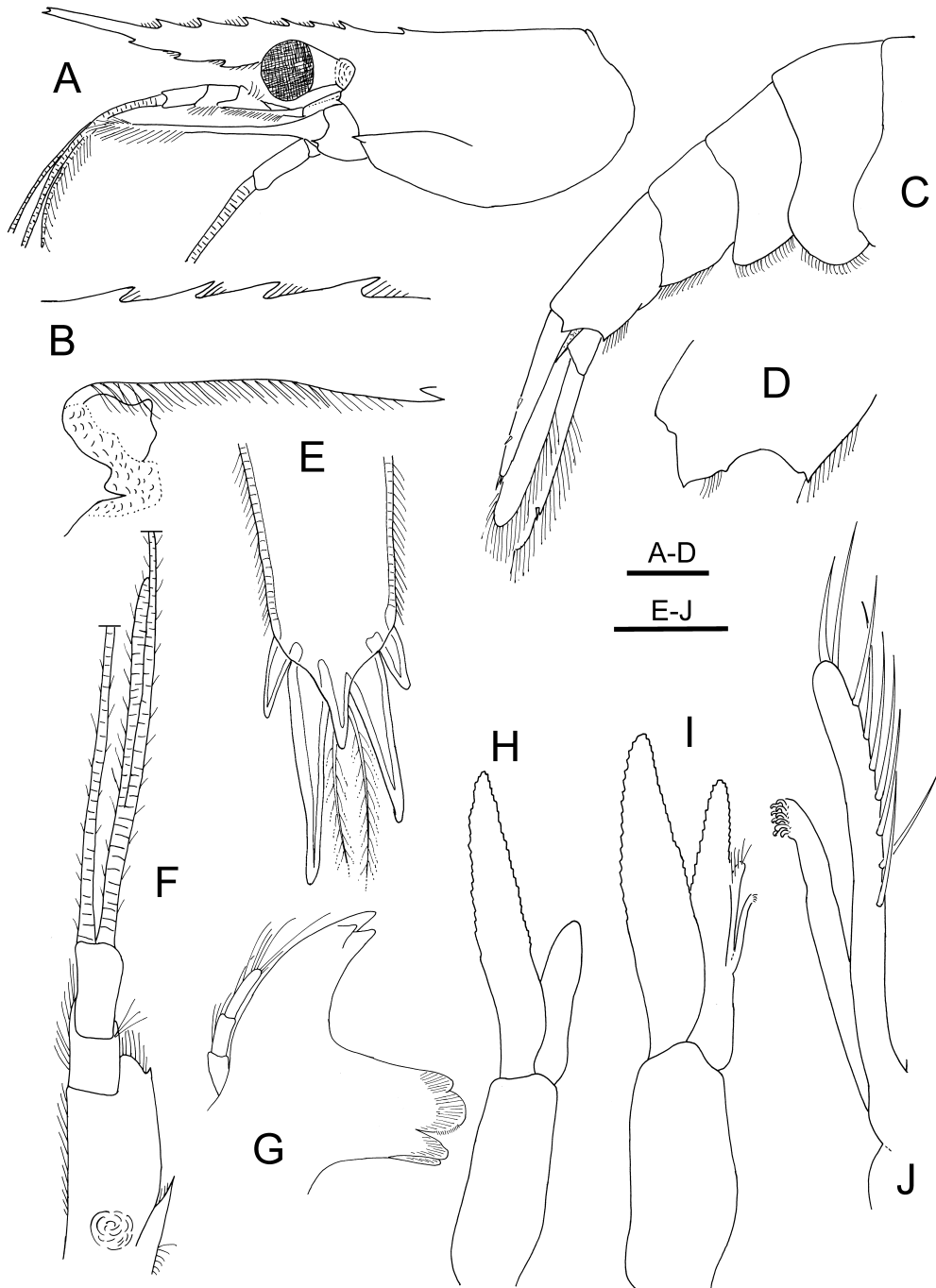
**Description.** – A small sized *Palaemon* species.

Carapace glabrous. Rostrum (Figure 1A) slender, straight or nearly so, without strong posterior ventral curve; approximately 1.2 times pochl., overreaching scaphocerite by at least 0.2 (occasionally up to 0.33) times length; armed with 7-8 dorsal teeth and 3-4 ventral teeth; proximal four dorsal teeth with weakly constricted bases, posterior most tooth situated behind orbit, about 1.5 times more distant than gaps between the other teeth, second tooth situated above or slightly behind margin of orbit; distal portion (approximately one third) unarmed but with bifid tip; double row of setae present in ventral unarmed portion, single row of setae present between the teeth. Antennal and branchiostegal teeth present, marginal. Branchiostegal groove originating dorsal to branchiostegal tooth, trending downwards and finishing just in front of half carapace length, slightly lower than at its origin. Sub-orbital lobe (Figure 1B) subquadrate to rounded, pterygostomial angle rounded. Bec ocellaire (Figure 1B) with strongly convex anterior margin, pronounced beak, almost pointing directly upwards, dorsal surface with strong concavity.

Eye (Figure 1A) well developed, with pigmented cornea; cornea slightly wider and longer than stalk; ocellus present on dorsomesial side.

Antennular peduncle (Figure 1F) extending to level of base of tooth of scaphocerite; basal segment 2.25 times as long as wide, slightly convex outer margin,





**Figure 1.** *Palaemon maculatus* (Thallwitz). Bonny River, Nigeria. USNM 181904. A. Frontal region, lateral. B. Same, eye removed. C. Abdomen, lateral view. D. Sixth pleonite, lateral view. E. Telson, distal part. F. Antennule. G. mandible. H. First pleopod, male. I. Second pleopod, male. J. Appendices masculina and interna. A-G ovigerous female, pocl 6.8; H-J male, pocl 4.8. Scale bars indicate 2.0 mm (A, C), 1.0 mm (B, D, F, H, I), 0.5 mm (J), 0.35 mm (E) or 0.25 mm (G).

stylocerite acute; antero-distal tooth falling short of laminar portion; inner ventro-mesial tooth present; statocyst with statolith; ultimate segment 2 times as long as penultimate, their combined length being slightly less than 0.75 times that of basal segment.

Dorsal flagellum of antennula fused for just under half its length (approximately 11-13 segments fused, 13-23 free); free portion with two aesthetascs on each segment.

Scaphocerite slender, laminar, 3.5 times as long as broad; outer margin straight terminating in tooth, falling short of distal margin of lamina; basal segment of antenna with large mesial tooth; antenna articulated to lateral margin of this segment. Flagellum of antenna about twice length of body.

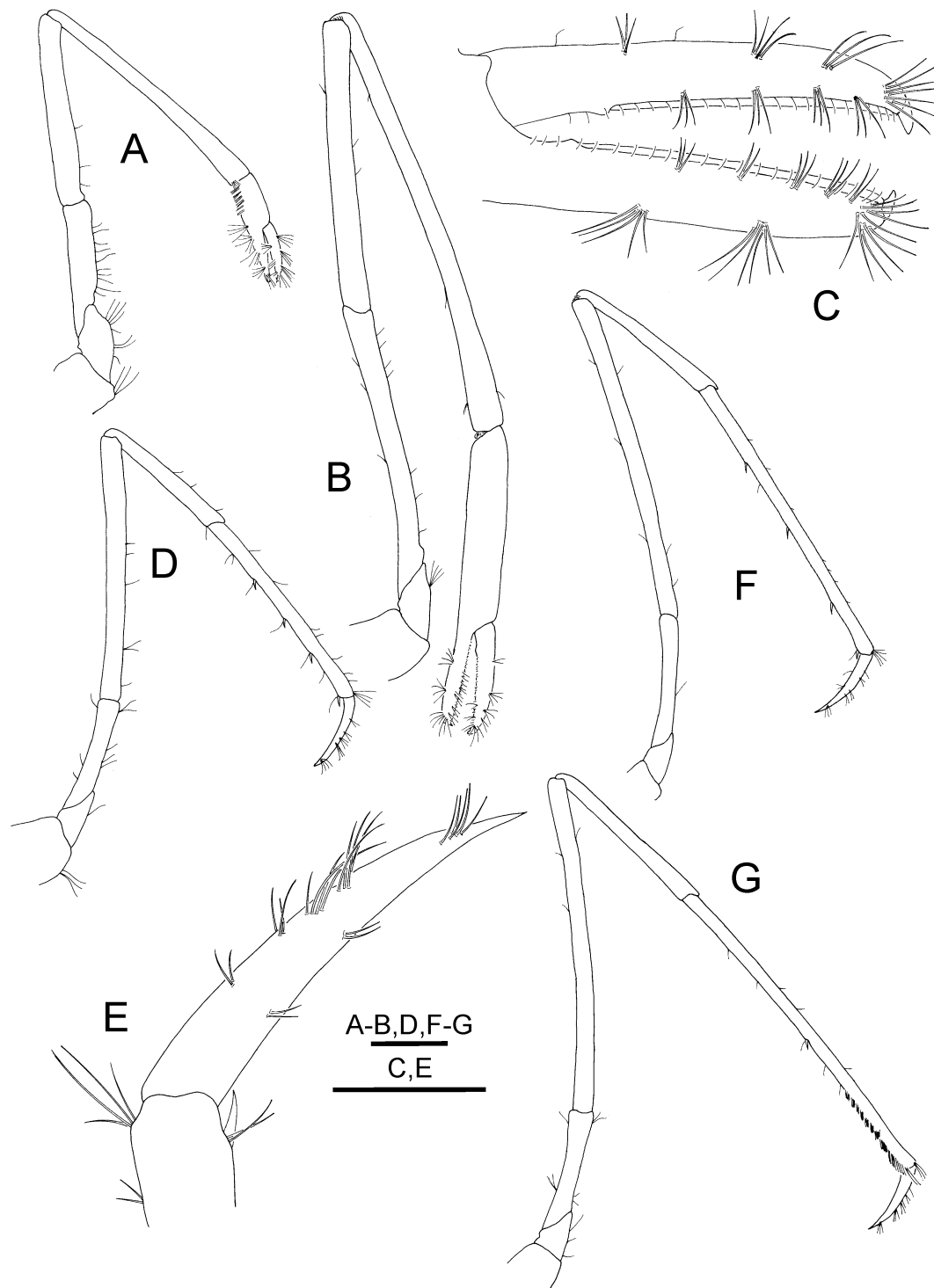
Abdominal pleurae furnished with plumose setae on ventral margin (Figure 1C); fifth pleuron posterodistal angle with distoventral tooth; sixth segment approximately 1.8 times length of fifth; lateral margin (Figure 1D) with small tooth and notch disto-ventrally; median lobe acute, with ventral submedian process.

Thoracic sternal armature sexually dimorphic. Fourth thoracic sternite in females armed with sharp tooth and incomplete posterior ridge, remainder with low transverse ridge; in ovigerous and post-ovigerous females eighth sternite with flattened setose plate. Fourth thoracic sternite in males with two lateral bosses.

Abdominal sternal armature sexually dimorphic. Females with blunt process on fourth abdominal sternite and acute longitudinal ridge on fifth; in males first abdominal sternite with small conical tooth, low transverse ridges present on second to fourth abdominal sternites; longitudinal ridge on fifth. Pre-anal carina unarmed in both sexes.

Mandible (Figure 1G) with three segmented palp in current material (but see remarks); terminal segment about 1.5 times as long as penultimate segment; penultimate and proximal segment approximately equal in length; terminal segment with 3 apical, simple setae and 4 lateral setae; penultimate segment bearing three distolateral setae. Incisor process of mandible with 3 teeth on right mandible, the middle of which is the smallest, and 4 teeth on left mandible, the middle 2 being smaller than the outer ones; molar process with 6 teeth of varying sizes. Paragnaths covering about half the mandibles; alae formed by broad, transverse more or less oval, distal lobes, ventromesial lobes triangular. Corpus short, narrowly separated; base with two posteriorly diverging carinae. Epistome triangular with rounded anterior

angle and strong anteromedial carina. Labrum broadly rectangular, flanked by triangular lobes on each side. Maxillula with lower lacinia near oval, smaller and



**Figure 2.** *Palaemon maculatus* (Thallwitz). Bonny River, Nigeria, ov. female (pocl 6.8). USNM 181904. A. First pereiopod. B. Second pereiopod. C. Same, chela. D. Third pereiopod. E. Same, dactylus. F. Fourth pereiopod. G. Fifth pereiopod. Scale bars indicate 1.0 mm (B, D, F-G), 0.7 mm (A), 0.5 mm (C) or 0.35 mm (E).

narrower than upper lacinia; upper lacinia provided with several distal cuspidate and stout setae; bearing a number of plumose setae on its upper margin; palp with bifid tip; upper process naked, lower process broad with two median setiform processes and small unfurnished ventral tubercle. Maxilla with upper lacinia deeply cleft, ending in a number of stout setae, a number of simple setae on its upper margin; palp well developed, broad and naked, except for a few plumose setae proximally on its outer margin; scaphognathite large, fringed with plumose setae; the lower lobe is broader than the upper. First maxilliped with endites separated by distinct notch; palp slender and slightly twisted; exopod well developed, slender and furnished with plumose setae distally; caridean lobe well developed and broad; epipod large and bilobed. Second maxilliped with slender rectangular ultimate segment; penultimate segment broadly triangular, with convex, semicircular upper margin; exopod well developed; well developed podobranch present. Third maxilliped pediform; ultimate segment 0.7 times length of penultimate; antepenultimate and preceding segment fused, with strongly curved dorsal margin; single, subdistal spine; exopod reaching to about 0.75 of length of antepenultimate segment; epipodal plate cupped, slightly prolonged anteriorly into a weak point; well developed arthrobranch and reduced pleurobranch present.

Well developed pleurobranchiae present on all thoracic legs. First pereopod (Figure 2A) overreaching scaphocerite by length of fingers; basis approximately 0.5 length of ischium; merus 1.5 length of ischium; carpus 1.3 times longer than merus; chela slightly less than 0.5 length of carpus, fingers slightly longer than palm, with tufts of setae; carpal-propodal brush well developed. Second pereopod (Figure 2B) extending beyond scaphocerite by full length of chela and just over 0.5 length of carpus; ischium 4.5 times length of basis; merus equal in length to ischium; carpus elongate, 1.5 length of merus; chela (Figure 2C) about 0.7 times length of carpus, approximately equal in length to the merus, fingers approximately 0.3 length of palm and covered in stout setae, poorly developed dentition proximally between fingers. Ambulatory pereopods increase in length, pereopod 3 being shortest. Third pereopod (Figure 2D) overreaching scaphocerite by 0.5 length of dactylus; ischium twice length of basis; merus 2.8 times length of ischium; carpus 0.5 length of merus; propodus 1.7 times length of carpus, slightly shorter than merus, ventral margin armed with 4-5 pairs of cuspidate setae; dactylus (Figure 2E) simple, about one third length of the propodus. Fourth pereopod (Figure 2F) overreaching scaphocerite by

0.2 of propodus; ischium slightly more than 2.5 times length of basis; merus 2.4 times length of ischium; carpus 0.5 length of merus; propodus 2 times length of carpus and approximately equal to merus, ventral margin provided with 5 pairs of cuspidate setae; dactylus 0.25-0.2 length of propodus. Fifth pereopod (Figure 2G) extending beyond distal margin of scaphocerite by 0.4 of propodus; ischium 2 times length of basis; merus 2.7 times length of ischium; carpus approximately 0.5 length of merus; propodus 2 times length of carpus and slightly longer than merus, ventral margin armed with 5 pairs of unevenly spaced cuspidate setae, grooming brush comprises 11 rows of serrulate setae and extends for about 0.3 length of propodus; dactylus 0.2-0.25 length of propodus.

First pleopod sexually dimorphic in proportions, lacking appendix interna in both sexes; in males (Figure 1H) endopod is 0.5 length of exopod, both exo- and endopods fringed with plumose setae but mesial portion of the inner margin of endopod devoid of plumose setae, with 6 spiniform setae; in females, endopod approximately 0.2 length of the exopod. Second to fifth pleopods broadly similar with the endopod being slightly shorter than the exopod, bearing an appendix interna. Second pleopod of males with appendix masculina; about 1.5 times length of appendix interna (Figure 1I and J), furnished with 7 lateral and 2 apical setae; lateral setae with minute setules, apical setae smooth.

Telson subequal in length to sixth pleonite; length:width ratio 4:1 proximally narrowing to 12.5:1 distally; dorsal surface with two pairs of cuspidate setae and 1 pair of simple setae subdistally on median process; proximal dorsal tuft of setae absent; proximal pair of cuspidate setae situated at about 0.4-0.5 of telson length, distal pair at about 0.7 length; marginal setae present along the full length; posterior margin (Figure 1E) prolonged into acute process, with 1 pair of plumose setae and 2 pairs of stout setae, inner pair about 4 times longer than outer pair; median process exceeding outer pair of stout setae.

Uropods broadly ovate, overreaching telson by 0.2 times length of endopod; exopod slightly longer than endopod, weak diarsis present; mobile lateral spine of exopod overreaching fixed tooth by length of tip.

Eggs numerous; 0.5x0.4 mm.

**Colour Pattern.** “Transparent shrimp lacking conspicuous pigment lines on carapace or abdomen (very faint lines may be present). Small but conspicuous black-and-white

pigment body in end of last abdominal segment. Eggs dull green. Pleura of ovigerous female with thin white ventral border” (Powell, 1983).

**Distribution and habitat.** Known from Senegal (Holthuis, 1980), Liberia (Rathbun, 1900; Johnston, 1906; Holthuis, 1952), Nigeria (Balss, 1916), Gabon (Thallwitz, 1892), Kabinda (Lenz, 1910), Congo (De Man, 1923, 1925; Schmitt, 1926) and Southern Angola (Balss, 1916). In fully marine and brackish water above about 10ppt, especially along quiet muddy shores (Powell, 1983).

**Remarks.** *Palaemon maculatus* is a highly distinctive species and not easily confused with any other of the genus found in the eastern Atlantic. The combination of the elongate carpus and palm of the chela of the second pereopod, the shape of the rostrum and the extent along the propodus and number of rows of setae of the grooming brush of the fifth pereopod allow for easy separation from other species found in the eastern Atlantic. Previous authors (De Man, 1925; Schmitt, 1926) have suggested that *P. maculatus* may be close to *P. longirostris* H. Milne-Edwards, 1837 and Rankin (1898) suggested a possible affinity with the western Atlantic *P. northropi* (Rankin, 1898). *Palaemon longirostris* differs in the shape of its rostrum and the number of rows of setae in the grooming brush of pereopod 5 (4 rows versus 11 in *P. maculatus*). *Palaemon northropi* has a strong pre-anal spine but also differs in the form of the rostrum. *Palaemon maculatus* may co-occur with *P. powelli* sp. nov.; differences between these two species are dealt with below (see remarks under *P. powelli* sp. nov.). *Palaemon elegans* has also been reported from the same geographic range as *P. maculatus* but may be distinguished by possessing a quadrate posterodistal angle of the fifth pleuron (versus small acute tooth in *P. maculatus*) and by having fewer rows of setae in its grooming brush on the propodus of pereopod 5 (4 rows in *P. elegans*).

This species was included in the subgenus *Palaeander* by Holthuis (1950). The subgenus is defined solely by the number of segments of the mandible palp (2 in *Palaeander*, 3 in *Palaemon s.s*) and is usually disregarded in taxonomic literature, following a number of studies that demonstrate infra-specific variability in this character in some species (Fujino & Miyake, 1968; Chace, 1972; Tirmizi & Kazmi, 1984). On the basis of the current material it appears that the mandible palp is usually three segmented concurring with the report of Schmitt (1926; also cited by Barnard,

1950). However, it is worthy of note that, one ovigerous female (pocl. 6.4 mm) examined here entirely lacks a mandible palp on the left hand side; on the right hand side a palp is present and three segmented. There is no evidence to suggest loss through damage so it is assumed that its absence is genuine. Based on Holthuis's (1950) observations, it would appear that the number of segments on the mandible palp may be variable in *P. maculatus* and cannot therefore reliably be used for species separation; however, a greater amount of material would need to be examined before the full extent of variability of this feature in *P. maculatus* can be described.

Schmitt (1926) comments on some variation between his material and that of other authors and some discrepancy is noted between his statements and the material examined here, notably in the proportions of the segments of the second pereopod and the range of rostral tooth counts. Schmitt states that 'the fingers of the second pair of legs are about two thirds the length of the palm' whereas in the present material the fingers are one third, occasionally slightly longer but never more than half, the length of the palm. De Man (1925) also figures a specimen in which the fingers are one third the length of the palm. Curiously, in the figure provided by Schmitt, which is based on that of Balss (1916), the fingers are clearly about one-third the length of the palm, contradicting his description. In the present material the dactyli of the fourth and fifth pereopods are 0.2-0.25 the length of the propodus, whereas Schmitt (1926) states they are one third and Thallwitz (1892) stated one half. The range of rostral teeth in the present specimens is 7-8(+1)/3-4. In material from the Congo, Schmitt (1926) reports that the range was 7-10/2-5, further stating that the extremes of these ranges are exceptional; it is assumed that Schmitt's counts included the subapical tooth but this cannot be said with certainty. Barnard's (1950) statement that the shorter ramus of the antennular flagellum is much shorter than the free part is based on Balss (1916, Figure 8). This is in agreement with Kemp (1925) but contradictory to De Man (1925) and Holthuis (1951), who found the fused and free parts to be equal, the original description of Thallwitz (1892) where the fused portion was described as longer than the free, and the present study, where it is fused for slightly less than half. The number of cuspidate setae on the ventral margin of the propodus of the ambulatory pereopods has not been mentioned by previous authors, except for Holthuis (1951) who simply stated 'a few spinules'. The number appears to be slightly variable in this species in contrast to other members of the genus where

the number seems to be fixed (pers. obs.). Occasionally these cuspidate setae were found to be lacking entirely.

Holthuis (1951) mentioned that a specimen reported as “*Leander adspersus*” from Liberia reported by Sharp (1893) may have been *P. maculatus* but as no description is given this cannot be stated with certainty. To our knowledge *Palaemon adspersus* has not been recorded as far south as Liberia.

The publication date of the original description of *P. maculatus* has variously been given as 1891 and 1892. On enquiry, the current editors of Arthropod Systematics and Phylogeny (previously *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden*) confirmed that the actual date of publication was 1892.

***Palaemon powelli* sp. nov.**

**Figures 3-8**

*Palaemon* species A. – Powell, 1983: 273, fig. 15.

*Palaemon* sp. – Powell, 1985: 235.

**Material Examined. Holotype:** ovigerous ♀, pochl. 7.7 mm; Oguck, 1 ft bank, ½ km from entrance to Bonny River, Niger Delta, Nigeria; 04°39'40"N 07°09'20"W; leg. C.B. Powell; NHM1980.325a. **Paratypes:** 5 ♂♂, pochl. 3.6 – 4.7 mm; 7 ♀♀, pochl. 4.6 – 6.5 mm; 4 ovigerous ♀♀, pochl. 5.8 – 6.5 mm; 1 juvenile pochl. 2.4 mm; same data as Holotype; NHM1980.325. 4 ♂♂, pochl. 3.6 – 4.8 mm; 5 ovigerous ♀♀, pochl. 5.9 – 7.6 mm; medium salinity mangrove creeks, Niger Delta; leg. C.B. Powell; RMNH.D 49892. 7 ♂♂, pochl. 2.2 – 4.1 mm; 4 ovigerous ♀♀, pochl. 5.5 – 6.0 mm; 18 ♀♀, pochl. 2.6 – 4.8 mm; medium salinity mangrove creeks, Niger Delta; leg. C.B. Powell; RMNH.D 49887. 2 ♂♂, pochl. 3.6 – 4.8 mm; 3 ovigerous ♀♀, pochl. 5.9 – 7.6 mm; medium salinity mangrove creeks, Niger Delta; leg. C.B. Powell; OUMNH-ZC 2008-01-0017.

**Comparative Material Examined.** *Palaemon adspersus*: 7 ♀♀, pochl. 6.3 – 10.3 mm; 2 ovigerous ♀♀, pochl. 10.5, 10.7 mm; Ria Formosa, Algarve, Portugal; 01/04/2004; leg. A. Whitaker; OUMNHZC 2004-16-0001.



*Palaemon longirostris*: 35 ♂♂, pochl. 5.4 – 9.5 mm; 3 ♀♀, pochl. 9.7 – 10.9 mm; Guadalquivir Estuary, Spain; 13/11/2004; leg. E. González-Ortegón; OUMNHZC 2005-03-0001. 11 ♂♂, pochl. 9.5 – 10.8 mm; 2 ♀♀, pochl. 12.3, 13.6 mm; Tilbury Power Station, Thames, UK; 51°27'6.5"N 0°23'19.0"E; 24/01/2007; leg. R. Kowalik; NHM 2008.872-881.

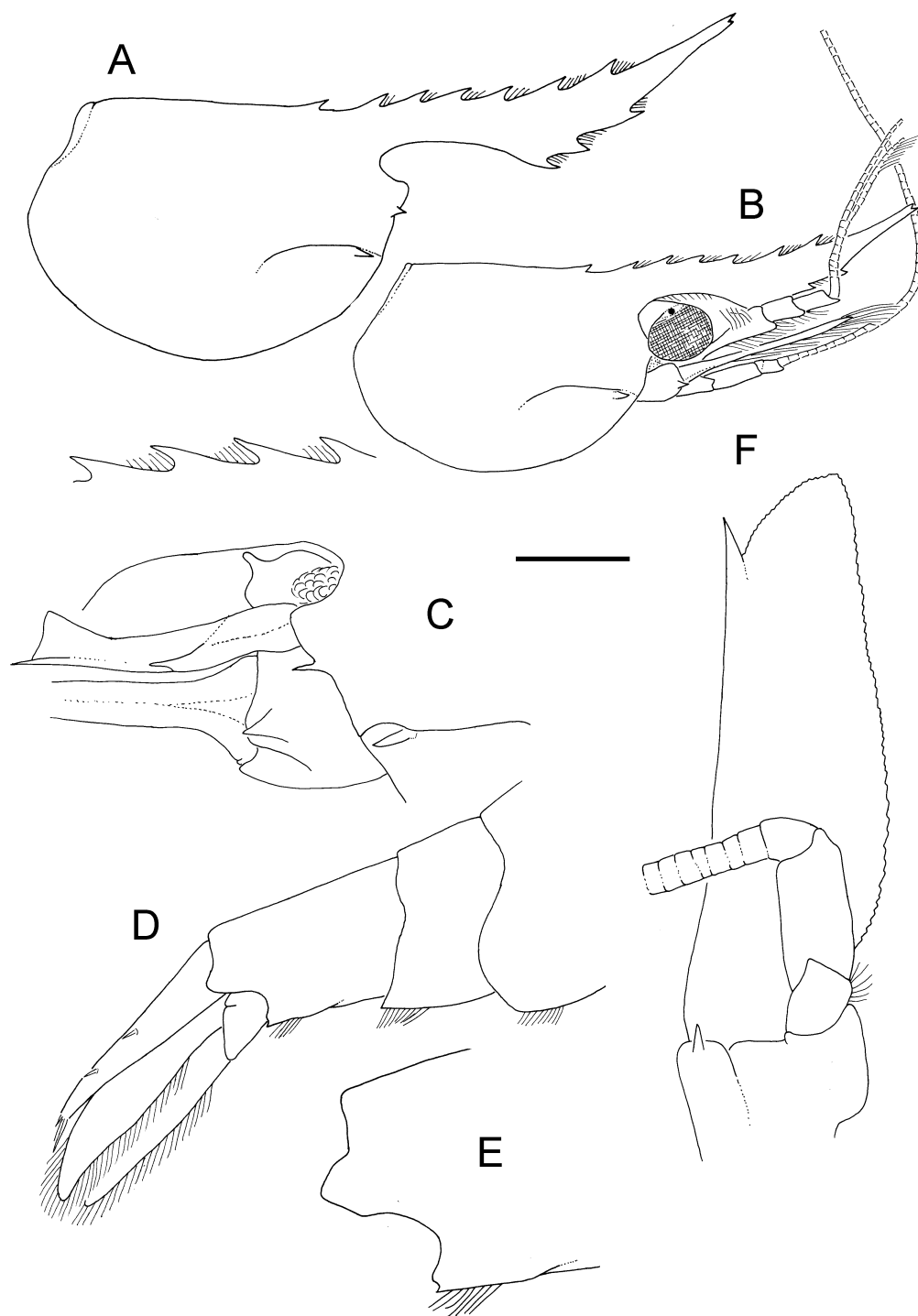
**Description.** – A small sized *Palaemon* species.

Carapace glabrous. Rostrum (Figures 3A-B, 8A-F) slender, ascendant in distal half, sometimes, slightly concave in middle; approximately equal to pochl., overreaching scaphocerite by 0.125 times length; armed with 6-8 dorsal teeth and 3-4 ventral teeth; proximal three dorsal teeth with weakly constricted bases; second tooth situated above or slightly behind margin of orbit; proximal most tooth 1.5 more distant than gaps between other teeth; distal portion (approximately one third) unarmed but with bifid tip. Double row of setae present in ventral unarmed portion, single row of setae present between teeth. Antennal and branchiostegal teeth present (Figure 3C); antennal tooth marginal, branchiostegal tooth variable in position, usually submarginal but may be slightly displaced from margin of carapace by up to 1-1.5 times its length. Branchiostegal groove originating dorsal to branchiostegal tooth, evenly curved and finishing just in front of half carapace length, slightly lower than at its origin. Sub-orbital lobe subquadrate (Figure 3C), pterygostomial angle rounded. Bec ocellaire (Figure 3C) with convex anterior margin, pronounced beak pointing upwards at approximately 45°, dorsal surface convex with slight anterior concavity.

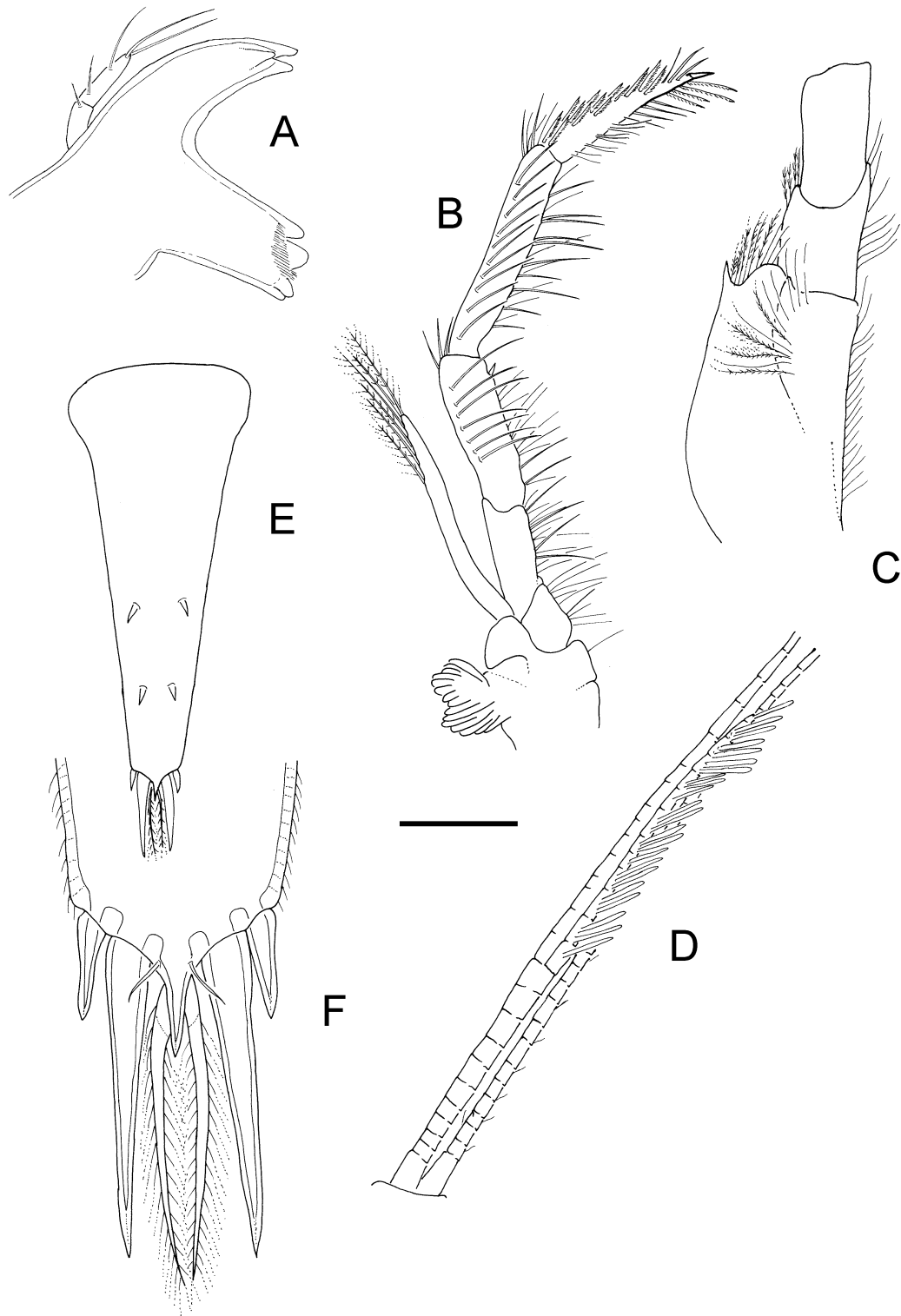
Eye (Figure 3B) well developed, with pigmented cornea; cornea slightly wider and longer than stalk; ocellus present on dorsomesial side.

Antennular peduncle (Figure 4C) extending to level with base of tooth of scaphocerite, or slightly further in males. Basal segment 2 times as long as wide with strongly convex outer margin, stylocerite acute; antero-distal tooth falling short of laminar portion; inner ventro-mesial tooth present; statocyst with statolith; ultimate segment 1.8 times as long as penultimate, their combined length being slightly less than 0.75 times that of basal segment.

Dorsal flagellum of the antennula (Figure 4D) fused for just under half its length (approximately 7-10 segments fused, 8-12 free); free portion bearing 2 or 3 aesthetascs per segment.



**Figure 3.** *Palaemon powelli* sp. nov., A. Carapace. B. Frontal region, lateral. C. Same, eye removed. D. Abdomen. E. Sixth pleonite. F. Antennal peduncle and scaphocerite. A-E holotype NHM1980.325a, F paratype NHM1980.325. Scale bar indicates 2.0 mm (D), 1.0 mm (E-F), 0.8 mm (A, C) or 0.5 mm (B)



**Figure 4.** *Palaemon powelli* sp. nov., paratype NHM1980.325. A. Mandible. B. Third maxilliped. C. Antennular peduncle, mesial view. D. Antennular flagella, proximal part. E. Telson. F. Same, distal part. Scale bar indicates 1.0 mm (B-E), 0.8 mm (A) or 0.5 mm (F).

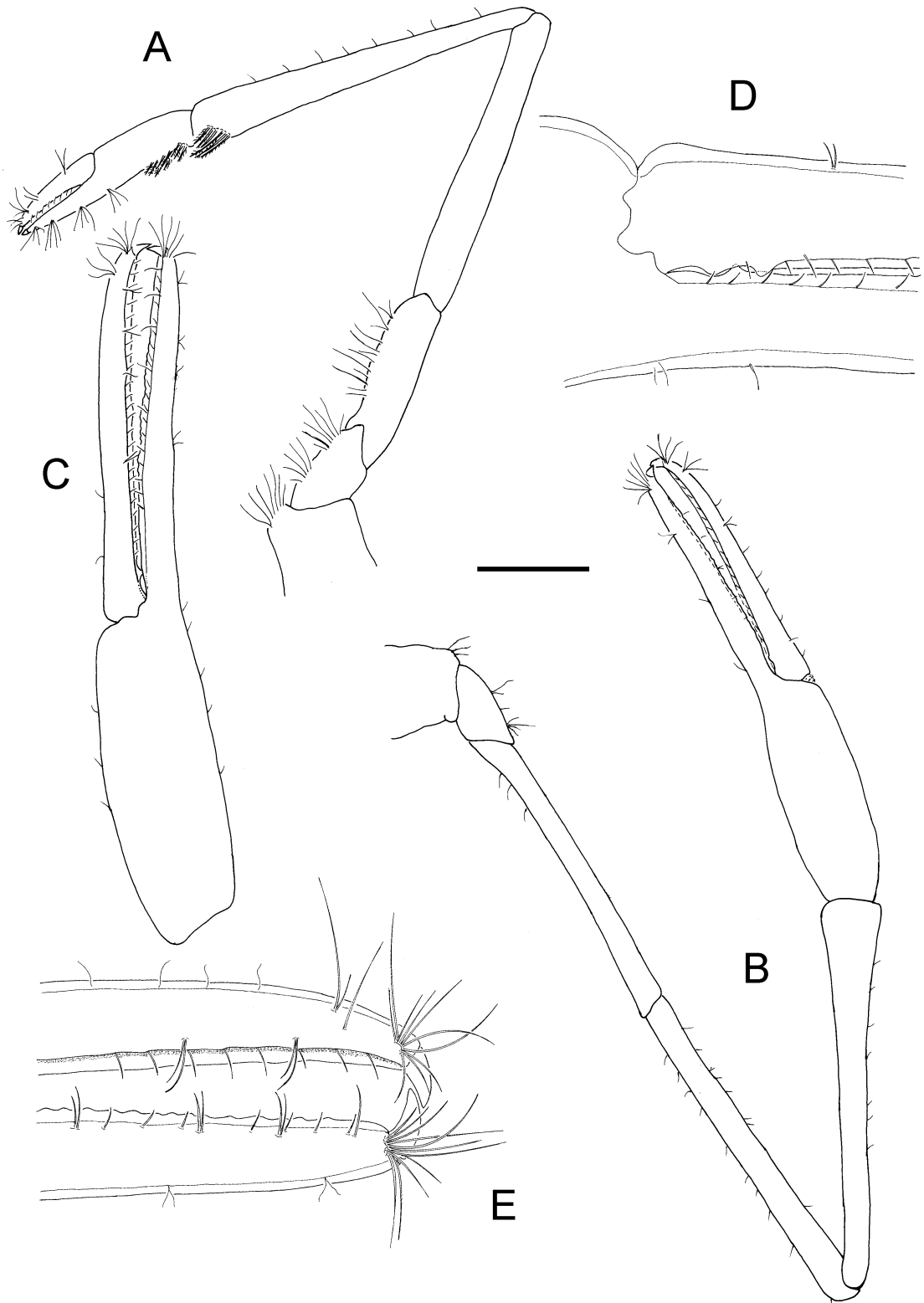
Scaphocerite (Figure 3F) laminar and just over three times as long as broad; outer margin straight or slightly concave terminating in tooth, falling short of distal margin of lamina; basal segment of antenna with large mesial tooth; antenna articulated to lateral margin of this segment. Flagellum of antenna about twice length of body.

Abdominal pleurae (Figure 3D) furnished with plumose setae on ventral margin; fifth pleuron posterodistal angle acute, sometimes prolonged into small laterally directed tooth; sixth segment approximately 1.5 times length of fifth; lateral margin (Figure 3e) with small tooth and notch disto-ventrally; median lobe blunt, lacking ventral submedian process.

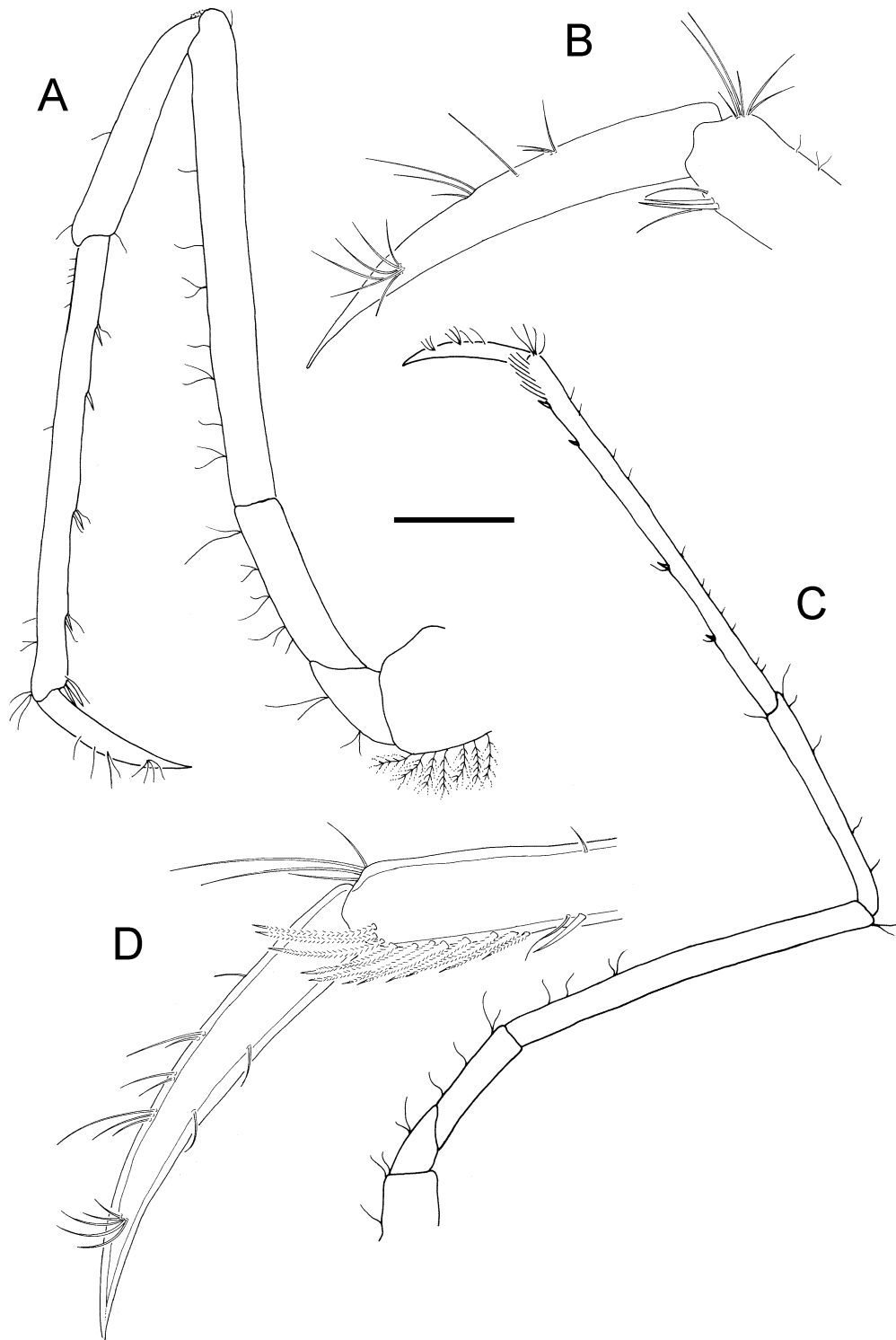
Thoracic sternal armature sexually dimorphic. Fourth thoracic sternite in females armed with sharp tooth, flanked by two submedian bosses, remainder with low transverse ridge; in ovigerous and post-ovigerous females eighth sternite with flattened setose plate. Eighth thoracic sternite in males with small, median tubercle.

Abdominal sternal armature sexually dimorphic. Females with blunt process on fourth abdominal sternite and acute longitudinal ridge on fifth; in males first to third abdominal sternite armed with broad flattened teeth with emarginated tips; longitudinal ridges present on fifth and sixth abdominal sternite. Pre-anal carina unarmed in both sexes.

Mandible (Figure 4A) with two segmented palp; terminal segment about 1.5-2 times length of proximal segment; terminal segment bearing two apical simple setae and two lateral setae; proximal segment with slightly swollen inner margin, bearing a single seta distally. Incisor process of mandible with 3 teeth on right mandible, the middle of which is the smallest, and 4 teeth on left mandible, the middle 2 of which are smaller than the outer ones; molar process with 6 teeth of varying sizes. Paragnaths covering about half the mandibles; alae formed by broad, transverse more or less oval distal lobes, ventromesial lobes triangular. Corpus short, narrowly separated; base with two posteriorly diverging carinae. Epistome triangular with rounded anterior angle and strong anteromedial carina. Labrum broadly rectangular, flanked by triangular lobes on each side. Maxillula with lower lacinia near oval, smaller and narrower than upper lacinia; upper lacinia provided with several distal cuspidate and stout setae but otherwise naked; palp with bifid tip; upper process naked, lower process broad with small ventral tubercle that bears a single recurved setiform process. Maxilla with upper lacinia deeply cleft, ending in a number of stout



**Figure 5.** *Palaemon powelli* sp. nov., paratype NHM1980.325. A. First pereiopod. B. Second pereiopod. C. Same, chela. D. Second pereiopod, chela, proximal. E. Same, distal. Scale bar indicates 1.0 mm (A, C), 0.7 mm (B) or 0.35 m (D, E.).

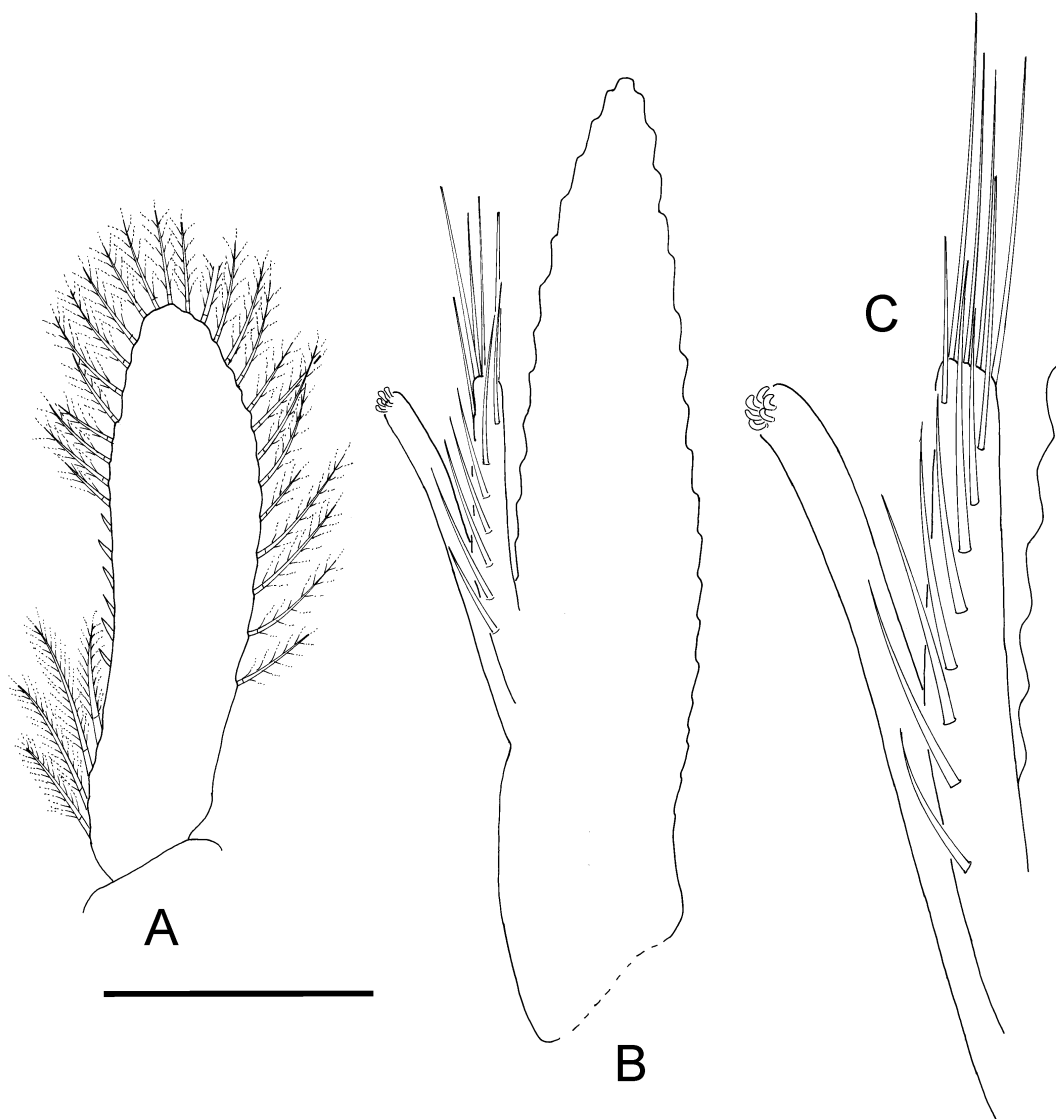


**Figure 6.** *Palaemon powelli* sp. nov., paratype NHM1980.325. A. Third pereiopod. B. Same, dactylus. C. Fifth pereiopod. D. Same, dactylus. Scale bar indicates 1.0 mm (A), 0.7 mm (C) or 0.35 mm (B, D).

setae, two simple setae on its upper margin; palp well developed, broad and naked except for a few plumose setae proximally on its outer margin; scaphognathite is large, fringed with plumose setae; lower lobe narrower than the upper. First maxilliped with endites separated by distinct notch; palp slender, slightly twisted and provided with single apical seta; exopod well developed, slender and furnished with plumose setae distally; caridean lobe well developed; epipod large and bilobed. Second maxilliped with slender rectangular ultimate segment; penultimate segment broadly triangular, with convex, semicircular upper margin; exopod well developed; well developed podobranch present. Third maxilliped (Figure 4B) pediform; ultimate segment 0.8 times length of penultimate; antepenultimate and preceding segment fused, with strongly curved dorsal margin; single spine subdistally; exopod reaches just over half length of antepenultimate segment; epipodal plate cupped, ear shaped; well developed arthrobranch and reduced pleurobranch present.

Well developed pleurobranchiae present on all thoracic legs. First pereopod (Figure 5A) overreaching scaphocerite by length of fingers and half palm; basis 0.5 length of ischium; merus 1.7 length of ischium; carpus slightly longer (1.1x) than merus; chela 0.6 times length of carpus, fingers approximately equal to palm, with tufts of setae; carpal-propodal brush well developed. Second pereopod (Figure 5B) extending beyond scaphocerite by full length of chela and 0.75 length of carpus; ischium 5 times length of basis; merus 1.1 length of ischium; carpus 1.1 length of merus; chela (Figure 5C-E) 1.25 times length of carpus, fingers about 1.2 times palm (but may be equal to palm in males and immature females), fingers slender, forcipitous, palm slightly swollen, strong dentition proximally between fingers (Figure 5D). Ambulatory pereopods increase in length, pereopod 3 being shortest. Third pereopod (Figure 6A) overreaching scaphocerite by 0.5 length of its dactylus; ischium 2 times basis; merus 2.5 times length of ischium; carpus 0.5 length of merus; propodus 2 times length of carpus, approximately equal to merus, ventral margin armed with 6 pairs of cuspidate setae; dactylus simple, about 0.3 length of propodus. Fourth pereopod overreaching scaphocerite by one sixth of its propodus; ischium 3 times length of basis; merus 2.8 times length of ischium; carpus 0.5 length of merus; propodus 2 times length of carpus and subequal to merus, ventral margin provided with 6 pairs of cuspidate setae; dactylus about 0.3 length of propodus. Fifth pereopod (Figure 6C) extending beyond distal margin of scaphocerite by 0.6 of propodus; ischium 2 times length of basis; merus 2.8 times length of ischium; carpus

0.6 length of merus; propodus 1.8 length of carpus and longer than merus, ventral margin armed with 6 pairs of unevenly spaced cuspidate setae, grooming brush comprises 2 rows of serrulate setae and extends for 0.1 length of propodus.



**Figure 7.** *Palaemon powelli* sp. nov., male paratype NHM1980.325. A. First pleopod, endopod. B. Second pleopod, endopod. C. Appendices masculina and interna. Scale bar indicates 0.5 mm (A-B) or 0.25 mm (C).

First pleopod sexually dimorphic in proportions, lacking appendix interna in both sexes; in males endopod 0.8 times length of exopod; both exo- and endopods fringed with plumose setae but mesial portion of inner margin of endopod devoid of plumose setae, with 6 spiniform setae (Figure 7A); in females, endopod



approximately one third length of exopod. Second to fifth pleopods broadly similar with endopod being slightly shorter than exopod, with appendix interna. Second pleopod of males with appendix masculina; appendix masculina subequal in length to appendix interna (Figures 7B-C), furnished with 8 lateral and 5 apical setae; both apical and lateral setae smooth; apical setae longer than lateral setae.

Telson (Figure 4E) approximately 1.2 times length of sixth pleonite; length:width ratio 2.8:1 proximally narrowing to 8.8:1 distally; dorsal surface with two pairs of cuspidate setae, proximal dorsal tuft of setae (few in number 2-4) and one pair of simple setae subdistally on median process; proximal pair of cuspidate setae situated at approximately 0.5 length, distal pair at 0.75 length; marginal setae present in distal portion only; posterior margin (Figure 4F) prolonged into acute process, with 1 pair of plumose setae, and 2 pairs of stout setae, inner pair more than 3 times longer than outer pair; outer pair finish approximately level with median process.

Uropods broadly ovate, overreaching telson by 0.2 times length of endopod; exopod slightly longer than endopod, weak diarsis present; mobile lateral spine of exopod overreaching the fixed tooth by length of tip.

Eggs numerous; 0.8x0.5 mm.

**Colour pattern.** “Transparent shrimp with thin dark transverse line across posterior edge of 3<sup>rd</sup> abdominal somite, more intense than any such line (if present) on other somites; and a short dark vertical (not oblique) line in middle of posterior half of side of carapace. Legs (including chelipeds) uncoloured, lacking reddish pigment at joints. Eggs dark olive, appearing black. Pleura of ovigerous females with 4 vertical bars (the last one an extension of the transverse abdominal line), with large conspicuous white patches” (Powell, 1983).

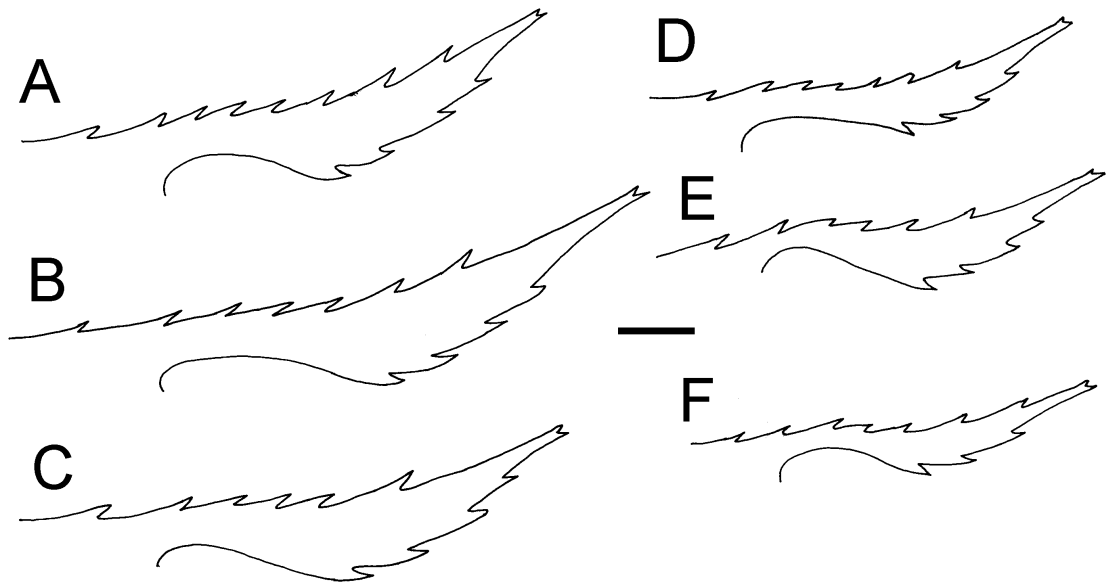
**Distribution and habitat.** Currently only known from medium salinity mangrove creeks in the Niger Delta, Nigeria. Powell (1983) states that it occurs in salinities between 5 and 20 ppt.

**Derivation of name.** The new species is dedicated to the collector of the type series, the late Charles Bruce Powell (1943-1998), in recognition of his work on the Decapoda of Nigeria. The name is genitive.

**Remarks.** *Palaemon powelli* sp. nov. is characterised by a combination of features. The shape of the chelae of the second pereopod, having the grooming brush of the fifth pereopod comprising just two rows of setae, the absence of a pre-anal spine and having the proximal most tooth of the dorsal rostral series 1.5 times removed are diagnostic for the species. A number of more subjective features may, likewise, have some diagnostic value; these include the relative length of the apical setae of the appendix masculina compared with the lateral series and the shape of the antennular peduncle.

In addition to *P. powelli* sp. nov. a further 12 species of *Palaemon* are reported from marine and brackish waters in the Atlantic: *P. adspersus* Rathke, 1837, *P. elegans*, *P. floridanus* Chace, 1942, *P. longirostris*, *P. macrodactylus* Rathbun, 1902, *P. maculatus*, *P. northropi*, *P. paivai* Filho, 1967, *P. peringueyi* Stebbing, 1915, *P. rosalesi* Rodriguez de la Cruz, 1965, *P. serratus* and *P. xiphias* Risso, 1816. With the exception of *P. adspersus*, *P. floridanus*, *P. longirostris* and *P. maculatus*, all these species possess a strong pre-anal spine easily separating them from *P. powelli* sp. nov. Currently, *P. paivai* and *P. roselesi* are poorly known and the pre-anal spine is not mentioned in their original descriptions. *Palaemon roselesi* (currently known only from Mexico) has a downwards sloping rostrum with dorsal teeth along its full length and *P. paivai* (from Brazil) has broad straight rostrum which would serve to separate them from *P. powelli* sp. nov. which has an upturned, slender rostrum that is unarmed distally. In *P. elegans* the pre-anal spine is occasionally reduced or lacking however it may be separated from the new species by having a quadrate versus acute posterodistal angle to its fifth abdominal pleura. *Palaemon powelli* sp. nov. can be separated from *P. maculatus* by the shape of the rostrum (upturned versus straight and slender), the proportions of the second pereopod (compare Figure 2b with Figure 5b) and the grooming brush of the fifth pereopod, which extends much further and comprises 11 rows of setae compared to 2 in *P. powelli* sp. nov. The western Atlantic, *P. floridanus* has a greater number of ventral rostral teeth than *P. powelli* sp. nov. (5-9 versus 3-4). From *P. adspersus* it can be separated by the shape of the rostrum (straight and broad in *P. adspersus* versus slender and upturned), the shape of the chelae (less elongate in *P. adspersus*) and the number of rows in the grooming brush on the propodus of pereopod 5 (4 rows in *P. adspersus* versus 2 rows in *P. powelli* sp. nov.). The taxonomy of *P. longirostris* is not fully resolved with González-Ortegón and Cuesta (2006) reporting two morphological forms. The northern form has a straight, deep

rostrum with dorsal teeth along its length and is not easily confused with *P. powelli* sp. nov. The southern form has a more slender and slightly upturned rostrum and is therefore more likely to be confused with the new species. It may be distinguished from *P. powelli* sp. nov. by the number of rows of setae in the grooming brush of the fifth pereopod (4 versus 2), the shape of the antennular peduncle as well as its larger size.



**Figure 8.** *Palaemon powelli* sp. nov., rostral variation NHM1980.325. A. Ov. female, pocl 4.6. B. Ov. female, pocl 5.0. C. Ov. female, pocl 4.6. D. Female, pocl 3.0. E. Female, pocl 3.4. F. Female (pocl 3.5). Scale bar indicates 1.0 mm.

As is normal in *Palaemon* (e.g. Yaldwyn, 1957; Gutu, 1971; De Grave, 1999; De Grave & Al-Maslmani, 2006), *P. powelli* sp. nov. shows variation in its rostrum shape and dentition. Some of this variation is shown in Figures 8A-F but this should be regarded as indicative rather than comprehensive. Although there are usually 3-4 ventral rostral teeth, one specimen (RMNH.D 49892) has 6 ventral teeth.

Powell (1983) provides a brief diagnosis of this species which is based largely on colour pattern (see description of colour pattern, above) but also he mentions some rostral features. The rostral features he mentions agree well with those described here.

Although undescribed, the presence of *P. powelli* sp. nov. in the Niger Delta has been known for many years and, in accordance with the suggestion of Powell (1983), some possible references to it are found in the literature as ‘*Palaemon* sp. A Powell’ (Marioghae, 1987; Ajayi et al., 1995; Adeyeye & Adubiaro, 2004). Despite its small size, Powell (1983, 1985) stated that *P. powelli* sp. nov. has some fisheries potential and is often present in catches of *P. maculatus* and there is evidence (Ajayi et al., 1995) that it may have limited commercial importance and may be a by-catch species of the fishery for *Nematopalaemon hastatus* (Aurivillius, 1898) although Marioghae (1987) suggests that the small size of this species makes it unsuitable for culturing.

### Acknowledgements

The authors would like to thank M. Lowe (NHM), K. Reed (USNM) and C. Fransen (Naturalis) for the loan of material. C. Fransen, C. d’Udekem d’Acoz and D. Pentcheff (NHMLAC) kindly provided difficult to access literature. C. Schmidt and Ch. Hebig of the journal “Arthropod Systematics and Phylogeny” provided the actual publication date of Thallwitz’s description of *P. maculatus*. M. Johnson (University of Hull) and T. Worsfold (Unicomarine) provided useful comments on an earlier draft of the manuscript.

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***Palaemon vicinus* sp. nov. (Crustacea: Decapoda: Palaemonidae), a new species of caridean shrimp from the tropical eastern Atlantic.**

**Abstract**

A new species of *Palaemon*, *P. vicinus* sp. nov., is described from the tropical eastern Atlantic. The new species is very close to *P. elegans* Rathke, 1837, under which name it was previously recorded from West Africa. *Palaemon vicinus* sp. nov. is easily separated from *P. elegans* by possessing a small tooth on the fifth abdominal pleuron (quadrate in *P. elegans*) and by having 2-3 rows of setae in the grooming brush of the fifth pereopod (4-5 in *P. elegans*). The discovery of the new species amongst material identified as *P. elegans* further highlights the need to reassess species level characters in the genus *Palaemon*.

**Introduction**

*Palaemon elegans* Rathke, 1837 was described on the basis of specimens from Sudak Bay, Ukraine, Black Sea (Rathke, 1837). The species has since been attributed a large geographic range in the eastern Atlantic, being reported from south-west Norway (Grieg, 1927, as *Leander squilla* (L., 1758)) extending southwards to southern Namibia [Lüderitz] (Balss, 1916, as *L. squilla*); including the Canary Islands (Holthuis, 1949), Cape Verde Islands (Holthuis, 1951; Türkay, 1982) and the Azores (Barrois, 1888 as *Palaemon squilla*); in addition it is also known from the whole of the Mediterranean and Black Seas (d'Udekem d'Acoz, 1999). The species has been recorded from West Africa by Osorio (1888), Ortmann (1893), Balss (1913), Stebbing (1914), Balss (1916), Schmitt (1926), Monod (1933), Holthuis (1951), Monod (1964), Türkay (1982) and Powell (1983; 1985), mostly under the name *Palaemon* (or *Leander*) *squilla* (Linnaeus, 1758). As with most *Palaemon* species, *P. elegans* shows a great degree of variation in some of the traditionally used taxonomic characters in the genus, throughout its reported range (De Man, 1915).

Specimens attributed to *Palaemon elegans* or *Palaemon* (or *Leander*) *squilla* from West Africa were examined and found to differ in a number of taxonomically important characters from specimens from close to the type locality, the

Mediterranean and North-West European locations, and are herein described as a new species.

The following abbreviations are used in the text: pocl (post-orbital carapace length), RMNH (Rijksmuseum van Natuurlijke Historie = Nationaal Natuurhistorisch Museum, Naturalis), Leiden), AMNH (American Museum of Natural History, New York), NHM (Natural History Museum, London), NMSZ (National Museums of Scotland, Zoology, Edinburgh) OUMNH-ZC (Oxford University Museum of Natural History Zoological Collection), USNM (United States National Museum of Natural History, Smithsonian Institution, Washington), ZMA (Zoological Museum, Amsterdam).

A restricted synonymy based on material examined in this study is provided below.

### **Systematics**

Family Palaemonidae Rafinesque, 1815

Subfamily Palaemoninae Rafinesque, 1815

*Palaemon* Weber, 1795

***Palaemon vicinus* sp. nov.**

### **Figures 1-7**

*Palaemon elegans* – Holthuis, 1952: 140 (only four of fourteen reported specimens examined. The identity of the remaining specimens requires investigation). – Powell, 1983: 272, fig. 14. – Powell, 1985: 235.

*Leander squilla* – Stebbing, 1914: 286.

**Type material.** – **Cape Verde.** – Holotype: ovigerous ♀, pocl. 6.8 mm; RMNH.D 53109; “Tydeman” Cancap-VII, Cape Verde Islands Expedition, Stn 7. K15, Boa Vista, W coast, NW coast of Ilhéu de Sal Rei; 16°10’N 22°58’E; intertidal (rockpool) and shallow sublittoral; protected area with sandy bottom, stones, boulders and corals; 27/28.viii.1986; leg. Cancap-VII expedition.

Paratypes: 1 ovigerous ♀, pochl. 6.5 mm; fully dissected; RMNH.D 53112; data as for holotype. – 1 ♂, pochl. 5.9 mm; RMNH.D 53110; data as for holotype. – 1 ♂, pochl. 5.1 mm; RMNH.D 53111; data as for holotype. – 11 ovigerous ♀♀, pochl. 5.9-7.5 mm, 9 ♀♀, pochl. 3.9-5.2 mm, 15 ♂♂, pochl. 3.4-5.6 mm; RMNH.D 51055; data as for holotype. – 7 ovigerous ♀♀, pochl. 6.4-7.7 mm, 2 ♀♀, pochl. 7.3-7.8 mm, 7 ♂♂, pochl. 5.5-6.9 mm; RMNH.D 51003; “Tydeman” Cancap-VII, Cape Verde Islands Expedition, Stn D15, São Vicente, W. Coast, Baia da Ribeirinha; 16°50’N 25°05’E; 07.vii.1986; leg. Cancap-VII expedition. – 3 ovigerous ♀♀, pochl. 7.0-7.4 mm, 1 ♀, pochl. 7.3 mm, 1 ♂, pochl. 6.1 mm; OUMNH-ZC 2009-07-0001; data as RMNH.D 51003.

**Non-type material. – Cape Verde.** – 1 ♀, pochl. 6.9 mm, 1 ♂, pochl. 6.0 mm; RMNH.D 21010; Bahia do Norte, São Vicente; 14.iii.1954; leg. Panelius. – 3 ♀♀, pochl. 4.1-6.1 mm, 1 individual damaged; NHM 1961.8.1.120-122; Stn 42, Praia, São Thiago; 13.xii.1945; leg. Atlantide Expedition. – 2 ovigerous ♀♀, pochl. 6.1, 6.4 mm, 7 ♀♀, pochl. 4.9-6.2 mm, 4 ♂♂, pochl. 3.1-5.0 mm; NMSZ 1921.143.875; Porto Grande, St. Vincent; 01.xii.1902. leg. Scottish National Antarctic Expedition. – **Nigeria.** – 3 ovigerous ♀♀, pochl. 5.8-7.1 mm; RMNH.D 49907; Niger Delta, creek mouth N of Isaka Seas School; 23.xii.1983; leg. C.B. Powell. – 1 ovigerous ♀, pochl. 7.4 mm, 1 ♀, pochl. 4.9 mm, 1 ♂, pochl. 5.3 mm; RMNH.D 15564; Niger Delta; v-vii.1960; leg. H.J.G. Beets. – 9 ovigerous ♀♀, pochl. 5.1-6.8 mm, 1 ♀, pochl. 6.5 mm, 13 ♂♂, pochl. 4.2-5.3 mm; RMNH.D 38519; Bonny River, 1 km N of Alochia, right bank N of entrance to creek, CBP stn. 141, 04°37’30”N 07°09’40”E, CBP stn. 140, 04°37’15”N 07°09’30”E; 13.v.1980; leg. C.B. Powell. – 8 ovigerous ♀♀, pochl. 5.2-6.2 mm, 1 ♀ pochl. 4.1 mm, 3 ♂♂, pochl. 3.6-4.0 mm; NHM 1980.327; Oroberekiri Creek, 2.25 km from entrance to Bonny River, Niger Delta, 04°40’05”N 07°10’10”; 29.vii.1980; leg. C.B. Powell. – 16 ovigerous ♀♀, pochl. 5.9-8.0 mm, 7 ♀♀, pochl. 3.1-7.1 mm, 19 ♂♂, pochl. 3.4-5.7 mm; USNM 181905; Bonny River, Hughes Channel, left bank, 1.7 km N of mouth of Boler Creek; 31.v.1980; leg. C.B. Powell. – **Sierra Leone.** – 1 ovigerous ♀, pochl. 6.9 mm; RMNH.D 10391; Kissy; by handnet; 11.viii.1955; leg. A.R. Longhurst. – **Gambia.** – 1 ovigerous ♀, pochl. 5.5 mm, 3 ♀♀, pochl. 3.4-3.8 mm, 34 individuals 1.7-2.4 mm; NHM 1951.4.3.2-11; Shallow rock pool, sandy bottom, Gunjur beach; 13.xi.1950; leg. M.H. Routh. – **Cameroon.** – 1 ovigerous ♀, pochl. 7.2 mm, 5 ♀♀, pochl. 3.4-5.5 mm, 15 ♂♂, pochl. 4.0-5.5 mm, 35

individuals, pocl 2.1-3.3 mm; RMNH.D 21732; Kribi; 10.iii.1964; leg. B de Wilde-Duyfjes.

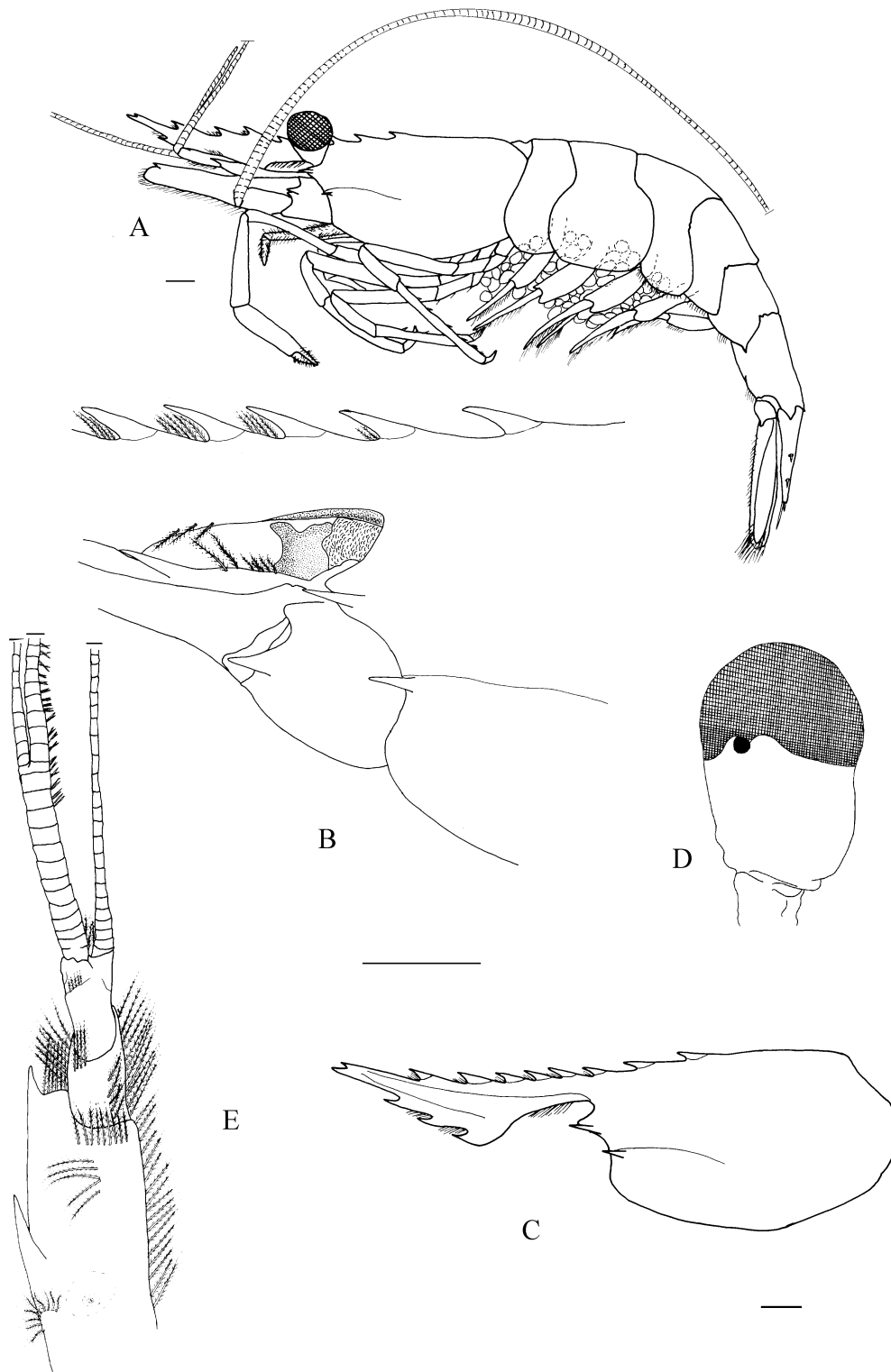
**Comparative Material.** *Palaemon elegans* – **Ukraine.** 2 ♀♀, pocl. 5.4, 6.2, 2 ♂♂, pocl. 5.2, 5.4 mm; ZMA Crust.De. 240252; Ukraine, Bay of Sebastopol; 1915; leg. S.A. Zernov; det. J.G. De Man. **Bulgaria.** — 3 ovigerous ♀♀, pocl. 10.6-11.2 mm; 7 ♀♀, pocl. 9.6-12.1 mm; 3 ♂♂, pocl. 6.8–7.6 mm; OUMNHZC 2008-01-0001; Varna; 31/05/2005-01/06/2005; leg. C.D. Schubart, S. Reuschel & S. Uzumova.

**Description.** – A small sized *Palaemon* species (Figure 1A).

Carapace glabrous. Rostrum (Figures 1C, 7A-I) deep, straight or slightly ascendant distally; slightly longer than carapace, overreaching scaphocerite by about 0.1 x length; armed with 8-11 (usually 9, rarely 11) dorsal teeth and 3 (rarely 4) ventral teeth; all dorsal teeth with weakly constricted bases, posterior three (occasionally two) teeth situated behind the orbit, the proximal most situated just in front of half carapace length; spacing between teeth roughly equal, although the proximal one is occasionally slightly more distant; distal portion (approximately 0.2) is usually unarmed but with bifid tip; double row of setae present in unarmed ventral portion, single row of setae present between the teeth. Antennal and branchiostegal teeth present, marginal. Antennal tooth slightly larger than branchiostegal tooth. Branchiostegal groove originating dorsal to branchiostegal tooth, trending downwards and finishing just in front of the mid-point of the carapace, slightly lower than at its origin. Sub-orbital lobe (Figure 1B) and pterygostomial angle rounded. Béc ocellaire (Figure 1B) with strongly concave anterior margin, pronounced upwardly directed beak, dorsal surface with strong concavity.

Eye (Figure 1D) well developed with pigmented cornea; cornea slightly wider than stalk but approximately equal in length; ocellus present on dorsomesial side.

Antennular peduncle (Figure 1E) extending to level of base of tooth of scaphocerite; basal segment 1.8 x as long as wide, slightly convex outer margin, stylocerite acute; statocyst with statolith; distolateral tooth of basal segment far exceeding laminar portion, almost extending to level of the distal margin of the penultimate segment; inner ventro-mesial tooth present; ultimate segment 1.5 x as long as penultimate, their combined length being slightly less than 0.85 x that of the basal segment; dorsal flagellum of the antennula fused for just under half its length



**Figure 1.** *Palaemon vicinus* sp. nov., A. whole animal in lateral view. B. frontal region, lateral view, eye removed. C. carapace, lateral view. D. eye, dorso-mesial view. E. left antennular peduncle, dorsal view. A, holotype RMNH.D 53109, B-E, female paratype RMNH.D 53112. Scale bars indicate 1.0 mm.

(approximately 11-12 segments fused, 12-14 free); free portion with two aesthetascs on each segment.

Scaphocerite (Figure 2A) slender, laminar, 3.5 x as long as broad; outer margin straight, terminating in a tooth, falling short of distal margin of lamina; basal segment of antenna with large lateral tooth. Flagellum of the antenna about twice the length of the body.

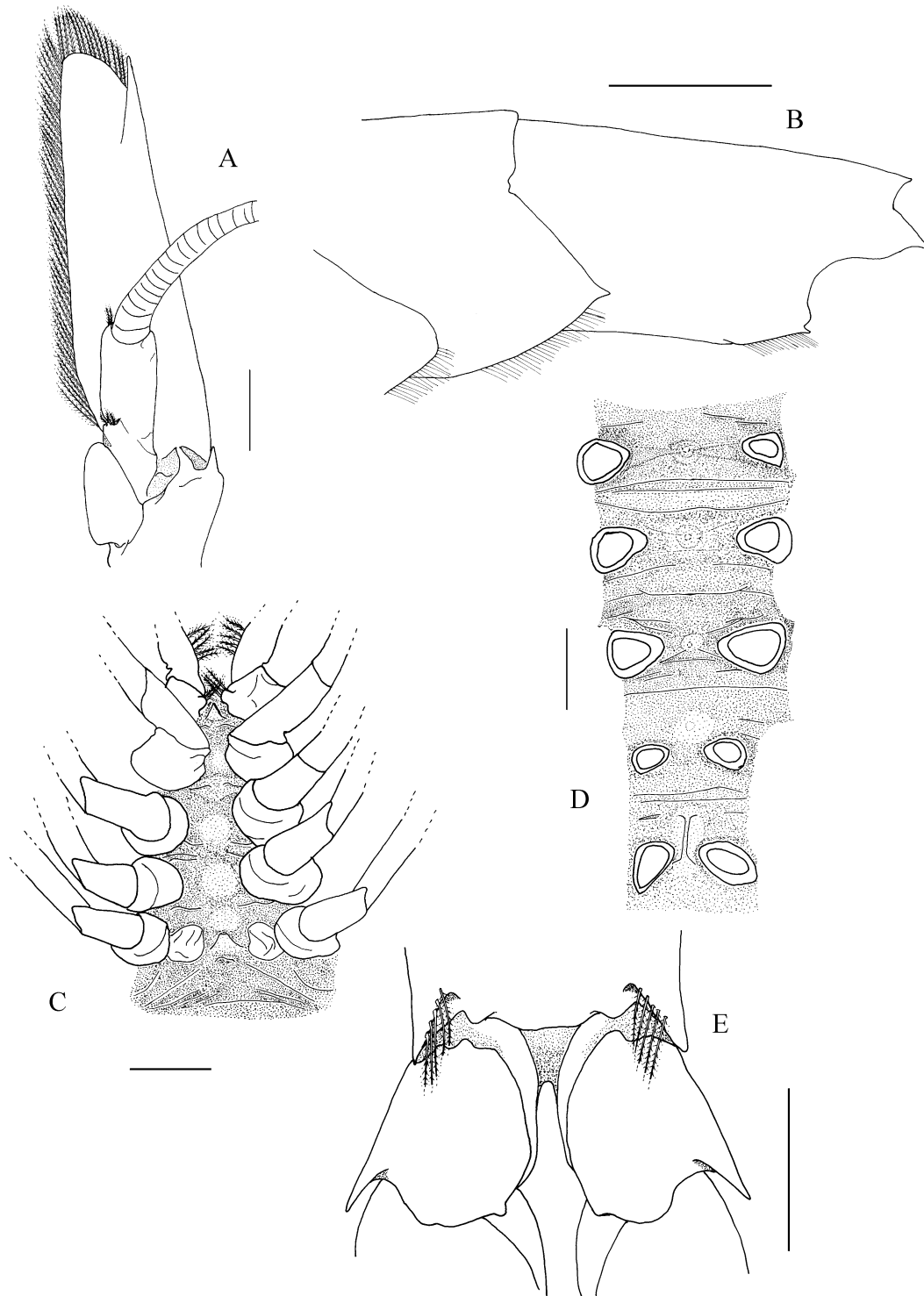
Abdominal pleura furnished with plumose setae on ventral margin (Figure 2B); fifth pleuron with distinct distoventral tooth; sixth segment is approximately 1.8 x length of fifth; posterolateral margin with small tooth and notch disto-ventrally; median lobe acute, with rounded ventral submedian process.

Thoracic sternal armature sexually dimorphic. Fourth thoracic sternite of females armed with a sharp tooth with a strong, incomplete posterior ridge, remainder with low transverse ridge; in ovigerous and post-ovigerous females eighth sternite with a flattened setose plate. Fourth thoracic sternite of males (Figure 2C) as in females, fifth to seventh thoracic sternites with low, rounded bosses and partial transverse ridges, eighth sternite with flattened tooth with an emarginated tip.

Abdominal sternal armature sexually dimorphic. First abdominal sternite of females with flattened tooth, second and third abdominal sternites armed with an acute tooth, fourth sternite unarmed, that of the fifth with a longitudinal ridge. In males (Figure 2D), first to third abdominal sternites bearing acute conical tooth; fourth abdominal sternite is a rounded boss occasionally bearing a small blunt tooth; fifth abdominal sternite as in females. Pre-anal plate (Figure 2E) unarmed in both sexes.

Epistome (Figure 4A) triangular with a rounded anterior angle and strong anteromedial carina; labrum narrow, rectangular, flanked by triangular lobes on each side. Paragnaths (Figure 4A) covering about half the mandibles; alae formed by broad, transverse more or less oval, distal lobes, ventromesial lobes triangular. Corpus short, narrowly separated; base with two carinae. Mandible (Figure 3A) with two-segmented palp; terminal segment equal to or slightly shorter than proximal segment; terminal segment with 5 simple, apical setae and 2 lateral setae; basal segment bearing two distolateral setae. Incisor process of mandible with 3 teeth on the right mandible, the central of which is the smallest, and 4 teeth on the left mandible, the inner 2 teeth being smaller than the outer ones; molar process with 6 teeth of varying sizes. Maxillula (Figure 3B) with lower lacinia near oval, smaller

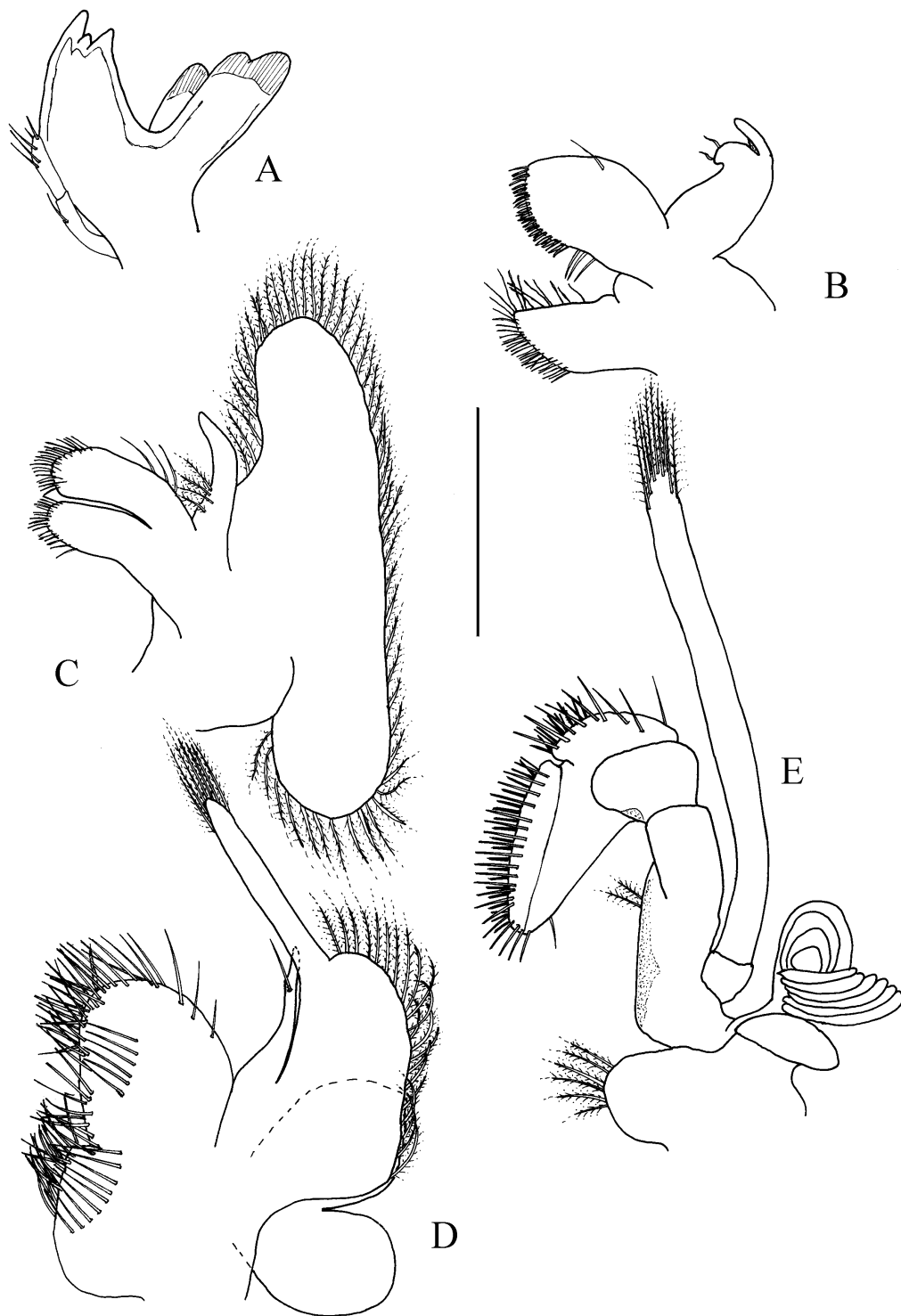




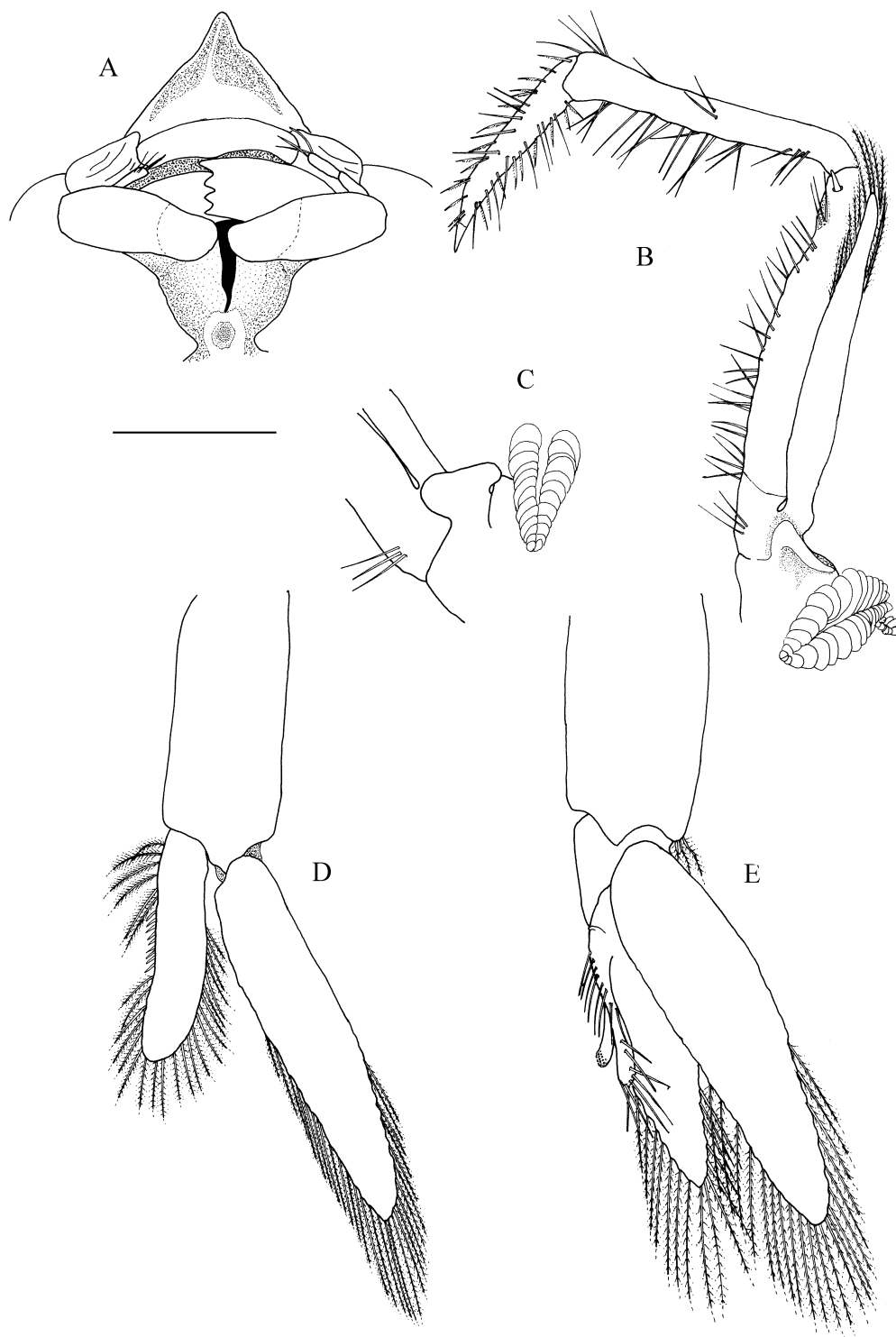
**Figure 2.** *Palaemon vicinus* sp. nov., A. left antennal peduncle and scaphocerite, ventral view. B. abdomen, lateral view. C. thoracic sternum, ventral view. D. abdominal sternum, ventral view. E. pre-anal plate, ventral view. A, female paratype RMNH.D 53112, B, holotype RMNH.D 53109, C-E, male paratype RMNH.D 53111. Scale bars indicate 1.0 mm.

and narrower than upper lacinia, bearing stout, plumose setae distally; upper lacinia is provided with several distal cuspidate and stout setae; with a few simple setae on its upper margin; palp with a bifid tip; upper process naked, lower process broad with one median setiform process and a further setiform process on the ventral tubercle. Maxilla (Figure 3C) with upper lacinia deeply cleft, ending in a number of stout, plumose setae, a number of simple setae proximally on its upper margin; palp well developed, broad and naked, except for a few plumose setae proximally on its inner margin; scaphognathite large, fringed with plumose setae; the lower lobe is broader than the upper. First maxilliped (Figure 3D) with endites separated by a distinct notch; palp slender and slightly twisted, with a single lateral simple seta; exopod well developed, slender and furnished with plumose setae distally; caridean lobe well developed and broad; epipod large and bilobed. Second maxilliped (Figure 3E) with a broad rectangular ultimate segment; penultimate segment broadly triangular, with a convex, semicircular upper margin; exopod much longer than endopod; epipod and well developed podobranch present. Third maxilliped (Figure 4B) pediform; ultimate segment 0.7 x length of penultimate; ischiomerus with strongly curved dorsal margin; a single spine subdistally; exopod slightly shorter than antepenultimate segment; epipodal plate (Figure 4C) ear shaped; well developed arthrobranch and a second, reduced arthrobranch present.

Well developed pleurobranchs present on all pereiopods. First pereiopod (Figure 5A) reaching tip of distolateral tooth of scaphocerite; basis approximately 0.6 length of ischium; ischium distoventrally expanded; merus 1.7 x length of ischium; carpus 1.3 x longer than merus and slightly expanded distally; chela 0.6 length of carpus, fingers slightly shorter than palm, with tufts of setae; carpal-propodal brush well developed. Second pereiopod (Figure 5B) extending beyond scaphocerite by half the length of the palm of the chela; ischium 2.0 x length of basis; merus 1.1 x length of ischium; carpus elongate, 1.1 x of merus, expanded distally; chela (Figure 5C) about 1.2 x length of carpus, fingers approximately 0.5 x length of palm and covered by stout setae, well developed dentition on proximal cutting edge of fingers (occasionally reduced). Ambulatory pereiopods similar, robust, increasing in length from third to fifth. Third pereiopod (Figure 5D) reaching tip of distolateral tooth of scaphocerite; ischium 1.4 x length of basis; merus twice length of ischium; carpus 0.45 length of merus; propodus 1.9 x length of carpus, slightly shorter than merus, ventral margin armed with 5 cuspidate setae, the distal most of which is paired, inner-



**Figure 3.** *Palaemon vicinus* sp. nov., A. mandible. B. maxillula. C. maxilla. D. first maxilliped. E. second maxilliped. All from female paratype RMNH.D 53112. Scale bar indicates 1.0 mm.

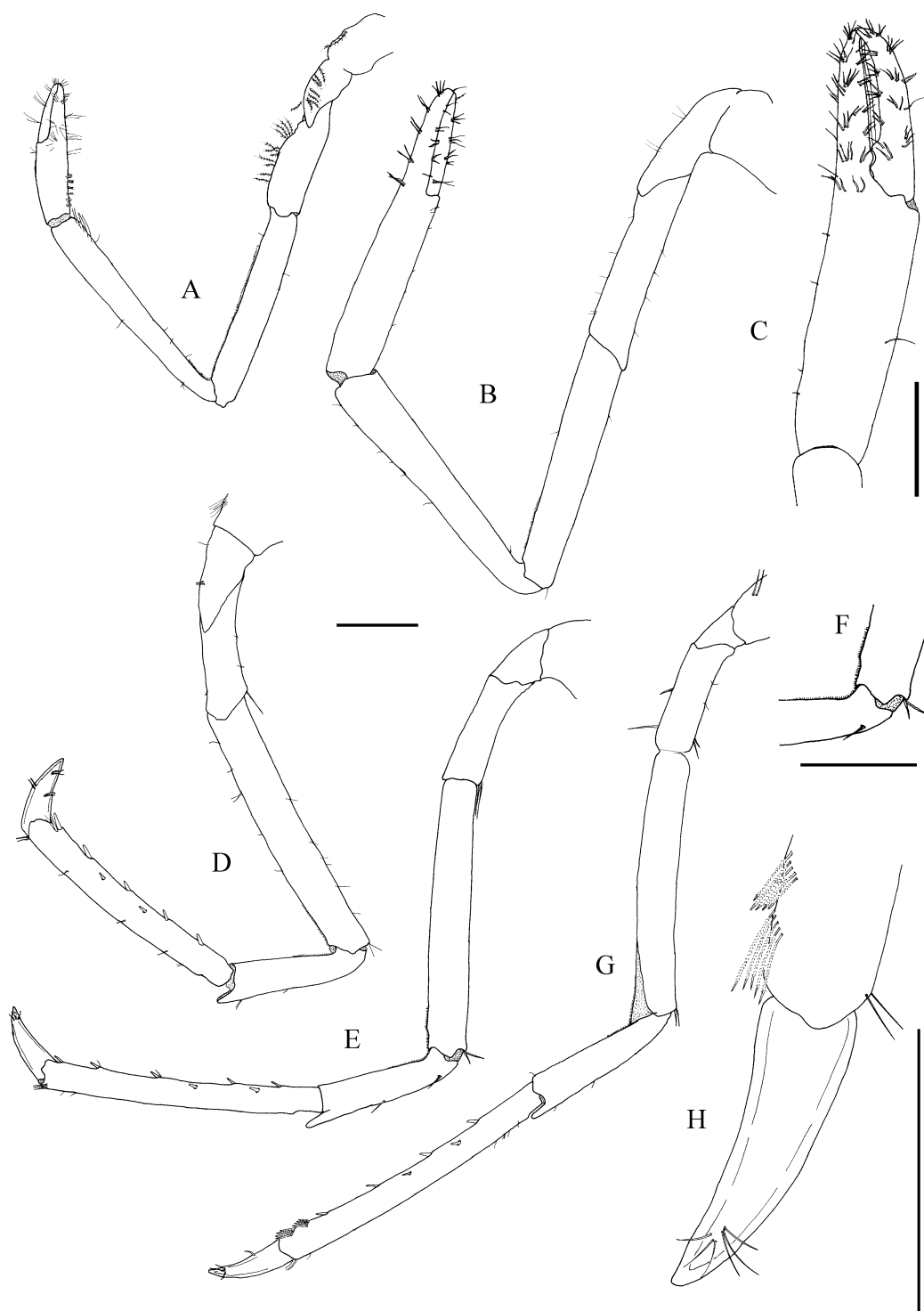


**Figure 4.** *Palaemon vicinus* sp. nov., A. epistome, labrum and paragnaths, ventral view. B. third maxilliped, lateral view. C. same, detail of epipodal plate. D. male left first pleopod, anterior view. E. male left second pleopod, anterior view. A-C, female paratype RMNH.D 53112, D and E, male paratype RMNH.D 53110. Scale bar indicates 1.0 mm.

ventro-lateral margin bearing 2 cuspidate setae; dactylus simple, stout, feebly curved, slightly more than one third length of the propodus. Fourth pereopod (Figure 5E) falling short of the distolateral tooth of the scaphocerite by at least half the length of the dactylus; ischium 1.5 x length of basis; merus 2.3 x length of ischium; carpus 0.5 length of merus; propodus slightly more than 2 x length of carpus and approximately equal to merus, ventral margin provided with 5 cuspidate setae, the distal most of which is paired, inner-ventro-lateral margin bearing 2 cuspidate setae; dactylus simple, stout, feebly curved, about one third length of propodus. Fifth pereopod (Figure 5G) extending to about half length of scaphocerite, to the level of the distolateral tooth of the antennular peduncle; ischium 1.4 x length of basis; merus 2.3 x length of ischium; carpus 0.6 length of merus; propodus 2 x length of carpus, ventral margin armed with 5 cuspidate setae, the distal most of which is paired, inner-ventro-lateral margin bearing 2 cuspidate setae, grooming brush (Figure 5H) comprises 2 (rarely 3 in larger individuals) rows of serrulate setae and extends for about 0.15-0.2 x length of propodus; dactylus simple, stout, feebly curved, slightly less than one third length of propodus. All pereopods have a fine pubescence at the carpo-meral joint (Figure 5F).

First pleopod sexually dimorphic in proportions, lacking appendix interna in both sexes; in males (Figure 4D) endopod is 0.6 length of exopod, both exo- and endopods fringed with plumose setae but mesial portion of the inner margin of endopod devoid of plumose setae, with 10 spiniform setae; in females, endopod approximately 0.3 length of the exopod. Second to fifth pleopods broadly similar with the endopod being slightly shorter than the exopod, bearing an appendix interna. Second pleopod of males (Figure 4E) with appendix masculina; about 1.25 x length of appendix interna (Figure 6A), furnished with 13-15 lateral and 5-10 apical setae; apical setae with minute setules.

Telson (Figure 6B) subequal in length to sixth pleonite; length:width ratio 3.3:1 proximally narrowing to 7.2:1 distally; dorsal surface with two pairs of cuspidate setae and 1 pair of simple setae subdistally on median process; proximal dorsal tuft of setae present, consisting of about 5 simple setae; proximal pair of cuspidate setae situated at about 0.4-0.5 of telson length, distal pair at about 0.7 of telson length; marginal setae present in distal portion only beginning at about the level of the anterior pair of cuspidate setae; posterior margin prolonged into acute median

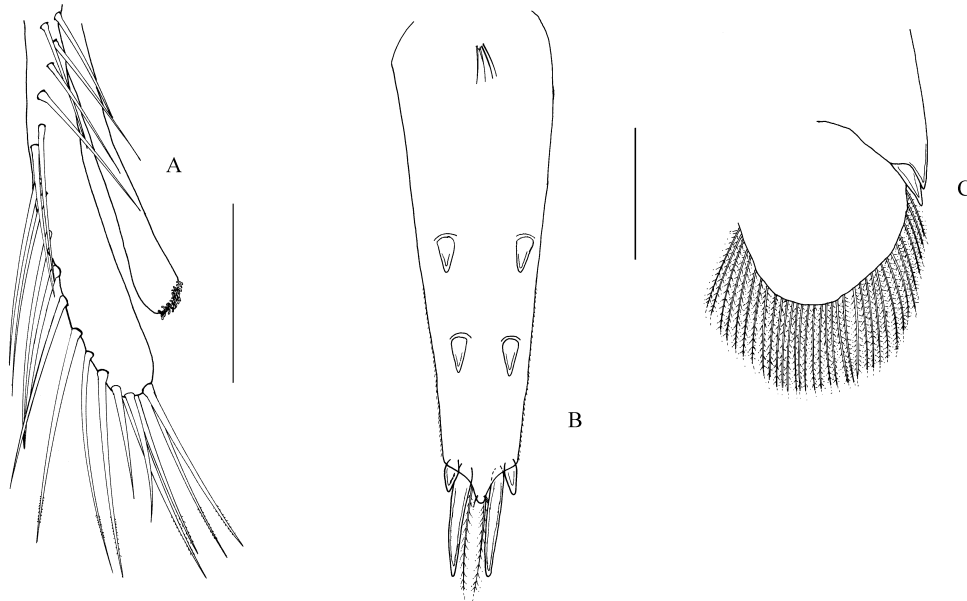


**Figure 5.** *Palaemon vicinus* sp. nov., A. first pereiopod, mesial view. B. second pereiopod, mesial view. C. same, chela. D. third pereiopod, mesial view. E. fourth pereiopod, mesial view. F. same, detail of carpo-meral joint. G. fifth pereiopod, mesial view. H. same, distal. All from female paratype RMNH.D 53112. Scale bars indicate 1.0 mm.

process, with 1 pair of plumose setae and 2 pairs of stout setae, inner pair about 4 x longer than outer pair; median process exceeding outer pair of stout setae.

Uropods broadly ovate, overreaching telson by 0.25 x length of endopod; exopod slightly longer than endopod, weak diarthrosis present; mobile distolateral seta of exopod overreaching fixed tooth by length of tip (Figure 6C).

Eggs with eye spots numerous; 0.8x0.6 mm.

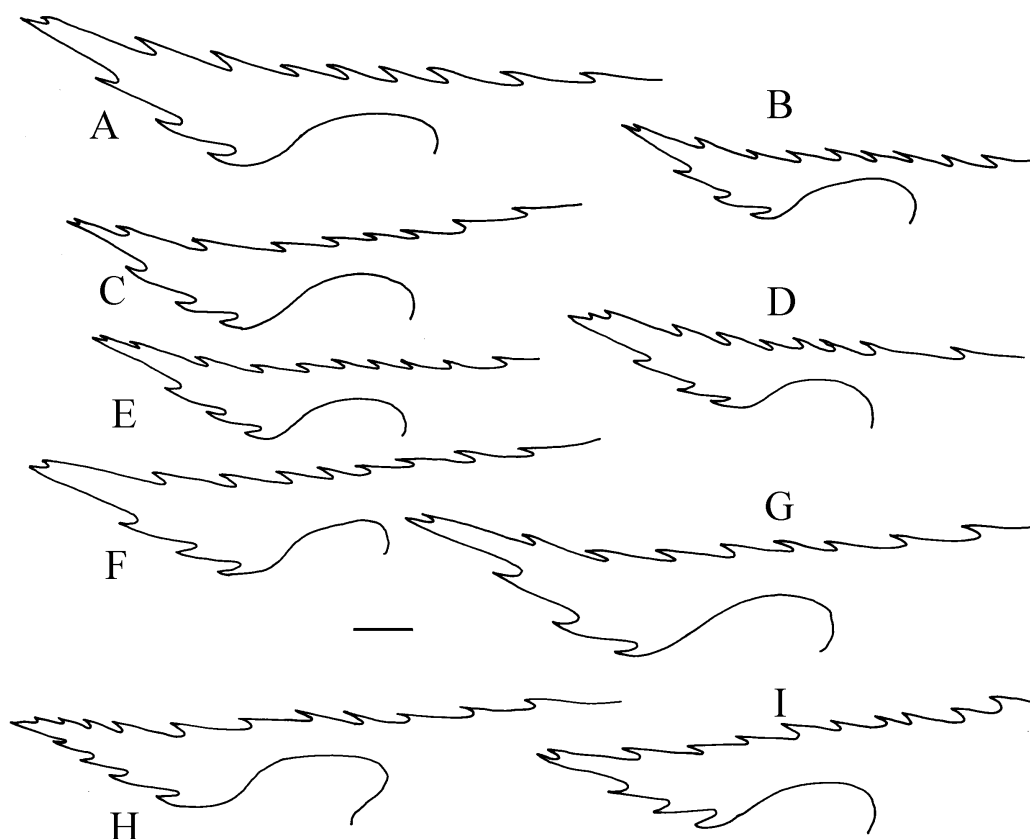


**Figure 6.** *Palaemon vicinus* sp. nov., A. appendix interna and appendix masculina. B. telson, dorsal view. C. uropod, close up of lateral tooth and mobile spine. A, male paratype RMNH.D 53110, B and C, female paratype RMNH.D 53112. Scale bars indicate 0.25 mm (A) and 1.0 mm (B and C).

**Colour pattern.** The following colour pattern description is based on Powell's (1983; p. 272) description of the colour pattern of *P. elegans*. His material is here referred to *P. vicinus* sp. nov. "Transparent shrimp with colour pattern of thin dark lines, several equally-intense transverse ones across the abdomen, and longitudinal and oblique ones on carapace; number of lines increasing with body size. Legs (including chelipeds) with reddish pigment at joints. Eggs green or brownish green. Pleura of ovigerous females bearing extensions of 4 dark vertical lines from the abdomen and some white patches".

**Distribution.** Currently known with certainty from Cape Verde, Gambia, Sierra Leone, Cameroon and Nigeria.

**Derivation of name.** *Vicinus*, -a, -um is a Latin adjective meaning near or neighbouring, alluding to the affinity between the new species and *P. elegans*.

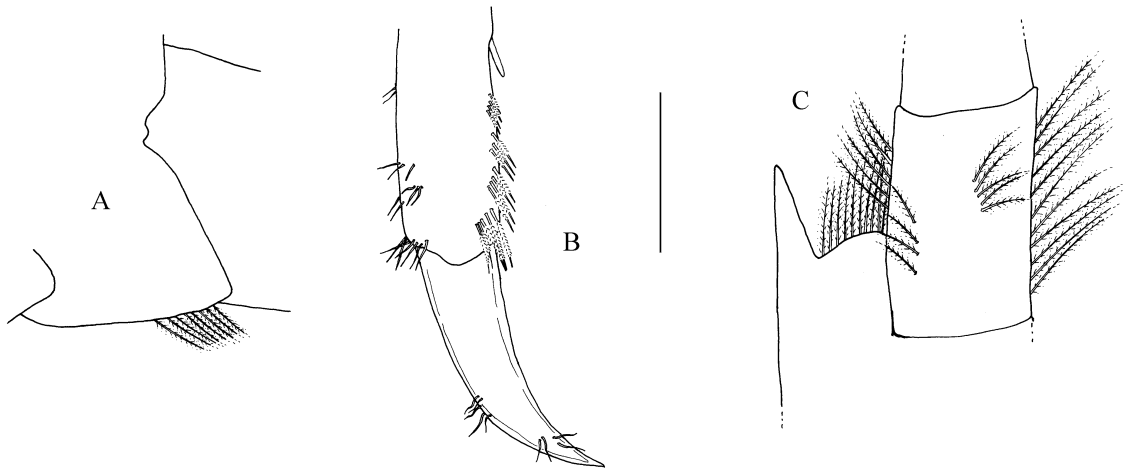


**Figure 7.** *Palaemon vicinus* sp. nov., rostral variation. A-G, from RMNH.D 51055, H and I, from RMNH.D 51003. Scale bar indicates 1.0 mm.

**Remarks.** *Palaemon vicinus* sp. nov. is undoubtedly closely related to *P. elegans*, under which name it has previously been recorded from West Africa. It primarily differs from *P. elegans* by the form of the postero-distal angle of the fifth abdominal pleura (prolonged into a small tooth in *P. vicinus* sp. nov., vs. quadrate in *P. elegans* compare Figure 2B with Figure 8A), the number of rows of setae in the grooming brush of the fifth pereopod (2-3 in *P. vicinus* sp. nov., vs. 4-5 in *P. elegans*, compare Figure 5H with Figure 8B) and subtle differences in the shape of the distal margin of the basal segment of the antennular peduncle (distolateral spine far exceeding anterior margin of laminar portion, extending almost to the distal end of the antepenultimate



segment, distal margin of laminar portion very slightly concave in *P. vicinus* sp. nov., vs. distolateral spine exceeding laminar portion, extending to about mid-level of the antepenultimate segment, distal margin of laminar portion with stronger concavity in *P. elegans*, compare Figure 1E with Figure 8C). *Palaemon vicinus* sp. nov. has a greater number of stout lateral setae on the appendix masculina of males (13 in *P. vicinus* sp. nov., vs. 10 in *P. elegans*) and slightly larger eggs of females (0.8x0.6 mm for *P. vicinus* sp. nov., vs 0.6x0.5 mm for *P. elegans* based on eyed embryos) than does *P. elegans*. In addition it is a very much smaller species than *P. elegans* with a maximum pocl amongst the specimens examined here of 6.9 mm for males and 8.0 mm for females vs. 11.2 mm for males and 19.1 mm for females of *P. elegans* (pers. obs.).



**Figure 8.** *Palaemon elegans* Rathke, 1837, A. fifth abdominal pleura. B. distal portion of fifth pereopod. C. antennal peduncle, dorsal view, close up of distal end of basal segment. All from female, pocl. 10.1 mm, from Varna, Bulgaria OUMNHZC 2008-01-0001. Scale bars indicate 2.0 mm (A) and 1.0 mm (B and C).

The new species is the tenth (including one non-native) species of *Palaemon* known from the eastern Atlantic. The other species are *P. adpersus* Rathke, 1837, *P. elegans* Rathke, 1837, *P. longirostris*, H. Milne-Edwards, 1837, *P. macrodactylus* Rathbun, 1902, *P. maculatus* Thallwitz, 1892, *P. peringueyi* (Stebbing, 1915), *P. powelli* Ashelby & De Grave, 2009, *P. serratus* Pennant, 1777 and *P. xiphias* Risso, 1816. Of these, *P. maculatus* and *P. powelli* are found in the same geographic range

as *P. vicinus* sp. nov. Powell (1983) specifically mentions *P. elegans* (his records are here attributed to *P. vicinus* sp. nov.) occurring with *P. maculatus* in the Niger Delta. The two species can be separated by the form of the rostrum (slender, with 7-8 dorsal teeth in *P. maculatus*, vs. broad, with 8-11 dorsal teeth in *P. vicinus* sp. nov.), the proportion of the carpus of the second pereopod (longer than chela in *P. maculatus*, vs. shorter than chela in *P. vicinus* sp. nov.) and the number of setal rows in the grooming brush of the fifth pereopod (11 rows in *P. maculatus*, vs. 2-3 rows in *P. vicinus* sp. nov.). From *P. powelli*, the new species can be separated by the form of the rostrum (typically more slender with fewer dorsal teeth and a longer unarmed distal portion in *P. powelli*) and the proportions of the fingers and palm of the chela of the second pereopod (fingers equal to or longer than palm in *P. powelli*, vs. about half the length of the palm in *P. vicinus* sp. nov.).

The fine pubescence at the carpo-meral joints of the pereopods noted here is not unique to *P. vicinus* sp. nov. (pers. obs.) but has not been previously described in any species of the genus.

Interestingly, one lot of specimens examined in this study (NHM1951.4.3.2-11) bears an internal label stating ‘? *Palaemon* (*Palaeander*) n. sp’ indicating that the collector and initial identifier, M.H. Routh, realised that they may represent a new species. An additional label provides the subsequent identification of *Palaemon* (*Palaeander*) *elegans*. Most of the individuals in this lot are very small and now in a poor state of preservation, however the larger individuals are unquestionably assignable to the present new species.

The possibility that the Banc d’Arguin may represent a biogeographical boundary has been suggested by Fransen (1991) and Spalding et al. (2007). The abiotic and ecological factors that may cause such a boundary are poorly understood (van Soest, 1993) but the area coincides with the meeting point of the southwards, cooling Canaries Current and the northwards, warming Guinea Current and these currents may play a role in determining the faunal distributions in the region. The matter still remains unresolved but, within *Palaemon*, it does seem to mark the southernmost limit of *P. serratus* (Pennant, 1777) and the approximate northern limit of *P. maculatus*. Although the colour pattern described by Powell (1983) for Nigerian shrimps identified as *P. elegans* shows some discrepancy with European specimens, photographs of *Palaemon* from Cape Verde Islands, kindly provided by Dr. Peter Wirtz, show individuals with a colour pattern similar to European specimens. As no

photo-matched specimens of *P. vicinus* sp. nov. are currently known it seems premature to rule out the occurrence of *P. elegans* in West Africa and further records of the species from tropical West Africa require confirmation before it is possible to speculate whether it occurs farther south than the Banc d'Arguin. Three of the four specimens of *Leander squilla* reported by Schmitt (1926) from St. Paul de Loanda, Angola (AMNH 4742) were re-examined and found to belong to *P. peringueyi*.

The fauna of tropical West Africa is clearly understudied and *P. vicinus* sp. nov. is the fourth caridean, and second species of *Palaemon*, to be described from tropical West Africa since 2008 (see also Anker et al., 2008; De Grave & Anker, 2008; Ashelby & De Grave, 2009). It is likely that other new species may be found through re-examination of museum material or fresh collections, particularly in cryptic habitats.

### Acknowledgements

The following people are gratefully acknowledged for making their specimens available for study: Charles Fransen and Jacques Smit (RMNH), Fiona Ware (NMSZ), Miranda Lowe (NHM), Dirk Platvoet (ZMA), Karen Reed (USNM), Mark Siddall and Sara Watson (AMNH). Peter Wirtz (Madeira) kindly sent photographs of West African *Palaemon*. Sammy De Grave (OUMNH) and Magnus Johnson (University of Hull) provided comments on an earlier draft of the manuscript that improved the quality of the final paper. The study was partially supported by Unicmarine Ltd.

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**A new genus of palaemonid shrimp (Crustacea: Decapoda: Palaemonidae) to accommodate *Leander belindae* Kemp, 1925, with a redescription of the species**

**Abstract**

A redescription of the little known shrimp *Leander belindae* Kemp, 1925 based on syntypical material as well as some previously unreported museum specimens is provided. In view of its aberrant morphology, a new genus, *Rhopalaemon* gen. nov., is erected. The new genus is most similar to *Palaemon* Weber, 1795, but can be easily distinguished from that genus, and all other palaemonine genera, by the following combination of characters: propodus of the ambulatory pereopods distally expanded; branchiostegal tooth and groove present; basal crest on rostrum absent; appendix interna on the first pleopod of males absent; and mandibular palp present.

**Introduction**

*Leander belindae* Kemp, 1925 was described on the basis of 75 specimens taken from rock pools at Kilakarai in the Gulf of Mannar and a further specimen taken from Cape Comorin. Additional collections of this species have been reported only twice since its description (Kurien, 1954, eleven specimens from Kanyakumari, Tamil Nadu; Ravindranath, 1979, nine specimens from Visakhapatnam, Andhra Pradesh) and, to the authors' knowledge, the species has only been mentioned in the literature (mostly as *Palaemon belindae*) six times following its description (Holthuis, 1950; Kurien, 1954; Dutt & Ravindranath, 1974; Ravindranath, 1979; Pereira, 1997; Jayachandran, 2001). Holthuis (1950) transferred the species to the genus *Palaemon* Weber, 1795 and most subsequent authors have accepted this generic placement. With the exception of Jayachandran's (2001) verbatim reproduction of Kemp's description, and short diagnoses provided by Kurien (1954) and Ravindranath (1979), the aforementioned references just cite the species name without providing further details and no further descriptive information is available for the species. Syntypes belonging to *L. belindae* present in the collections of the Natural History Museum (London) and the Rijksmuseum van Natuurlijke Historie, Leiden (= Nationaal

Natuurhistorisch Museum, Naturalis) as well as some previously unreported specimens held in the Museum National d'Histoire Naturelle, Paris (MNHN) provide the opportunity to redescribe the species. A re-examination of these specimens has revealed that the species cannot be satisfactorily be included in either *Leander* Desmarest, 1849 or *Palaemon* as they are presently defined, nor any of the other Palaemoninae genera, and therefore a new genus is erected here to accommodate the species.

The following abbreviations are used in the text: pocl (post-orbital carapace length), ov. (ovigerous), RMNH (Rijksmuseum van Natuurlijke Historie = Nationaal Natuurhistorisch Museum, Naturalis, Leiden), NHM (Natural History Museum, London), MNHN (Museum National d'Histoire Naturelle, Paris).

### **Systematics**

#### **Palaemonidae Rafinesque, 1815**

#### **Palaemoninae Rafinesque, 1815**

#### ***Rhopalaemon* gen. nov.**

Type species: *Leander belindae* Kemp, 1925.

**Diagnosis.** Body subcylindrical, slightly compressed laterally. Rostrum laterally compressed, shorter than carapace, stout, without basal crest, with strong lateral ridge, with dorsal and ventral unarticulated teeth, single row of plumose setae present between the teeth. Carapace glabrous with antennal and branchiostegal teeth, branchiostegal groove arising dorsally to branchiostegal tooth. Branchiostegal tooth sub-marginal. Eyes pigmented, banded, with ocellus. Fourth thoracic sternite with well developed median process; eighth thoracic sternite of males with well developed process, that of females with small blunt tubercle. Well developed pre-anal tooth present. Mandible with palp, third maxilliped lacking subdistal spine on antepenultimate segment, other mouthparts as for *Palaemon*. Pereiopod 2 stout, being only slightly longer than ambulatory pereiopods. Pereiopods 3–5 with propodus

distally expanded bearing 3–5 strong spines distally; distal most spines paired; dactyli simple, strongly curved. Grooming brush on pereopod 5 reduced to a single poorly defined row hidden amongst the stout spines. Pleopod 1 of male without marginal appendix, with inner medial spines. Pleopods 2–5 with appendix interna in both sexes, pleopod 2 of male also with appendix masculina. Upper flagellum of antennula biramous, with rami fused for one quarter of their length. Antennular peduncle comprised of three articles, with well developed stylocerite, ventromedial tooth and anterodistal tooth present; statocyst present. Béc ocellaire well developed with strong median process. Fifth abdominal pleuron rounded posteroventrally. Telson with 2 pairs of dorsal spines situated dorsomedially; acute posteromedian process, 2 pairs of spines on posterior margin, outer pair much shorter than inner pair; 1 pair of very stout plumose setae, longer than inner pair of spines. Mobile medial spine of exopod of uropod slightly exceeding fixed tooth.

Gill formula as follows: 5 pleurobranchs (P1–5), 2 arthrobranchs (1 reduced, both Mxp3), 1 podobranch (Mxp2), 3 epipods (Mxp1–3), 3 exopods (Mxp1–3).

**Derivation of name.** The name is a combination of the Latin *rhopalon* meaning club like and the generic name *Palaemon* in reference to the club-like shape of the propodi of the ambulatory pereopods; gender masculine.

**Remarks.** The subfamily Palaemoninae currently contains 20 genera. Many of the generic diagnoses within this subfamily depend heavily on the presence and absence of a “hepatic” versus “branchiostegal” tooth. However, as pointed out by Walker and Poore (2003) these two teeth are in fact homologous structures, with the “hepatic” tooth merely being a branchiostegal tooth which has migrated further up the carapace during ontogeny. Notwithstanding this, the actual position of the tooth can continue to be used in differentiating genera.

The branchiostegal position of the tooth in the new genus, clearly differentiates it from *Brachycarpus* Spence Bate, *Macrobrachium* Spence Bate, *Neopalaemon* Hobbs and *Pseudopalaemon* Sollaud (in which the tooth is in a hepatic position), as well as from *Troglocubanus* Holthuis, *Troglomexicanus* Villalobos, Alvarez and Iliffe, *Troglindicus* Sankolli and Shenoy, *Leptocarpus* Holthuis and *Cryphiops* Dana (all these genera lack a branchiostegal tooth). *Rhopalaemon* gen. nov. can be differentiated from both *Exopalaemon* and *Nematopalaemon*, as it lacks the dorsal, rostral crest, characteristic of both these genera. The presence of a distinct branchiostegal groove further separates the new genus from *Leandrites* Holthuis,

*Creaseria* Holthuis, *Urocaridella* Borradaile and *Leander* Desmarest, in which such a groove is lacking.

*Rhopalaemon* gen. nov., appears closely related to a rather heterogeneous assemblage comprised of *Coutierella* Sollaud, *Palaemonetes* Heller and *Palaemon* Weber. The relationships between these genera (and their constituent species) are poorly understood at present. *Coutierella* differs considerably from the other genera in the structure of its mouthparts. The laciniae of the maxillula are broad, the lower one being twisted, whilst the basal endite of the maxilla bears a fringe of very long setae; these and other differences clearly indicate an adaptation to a specific food source (see Bruce, 1989). In contrast, the mouthparts are rather conservative in *Palaemon*, *Palaemonetes* as well as *Rhopalaemon* gen. nov. Although *Palaemonetes*, as currently defined, lacks a mandibular palp (vs. present in *Rhopalaemon* gen. nov.), the validity of this character has been questioned (Fujino & Miyake, 1968; Chace, 1972).

*Rhopalaemon* gen. nov. primarily differs from both *Palaemon* and *Palaemonetes* in the conspicuous development of the distal part of the propodi of the ambulatory pereopods, these being ventrally expanded (vs. not-developed); furnished with a concentrated row of stout spines (vs. dispersed along the medial margin); as well as the very reduced grooming brush on the fifth pereopod (vs. comprised of at least two, distinct rows of serrulate setae). The development of the distal part of the propodi is reminiscent of those encountered in the unrelated genera *Rapipontonia* Marin (Pontoniinae), *Chlorocurtis* Kemp (Pandalidae), as well as in some species of *Thor* Kingsley and *Hippolyte* Leach. Although the precise function of this structure remains unclear, Marin (2007) suggested a grasping function to hold onto hydroids for *Rapipontonia*. A similar function could perhaps be inferred in *Rhopalaemon* gen. nov., although many species of *Palaemon* also live in hydrodynamically active environments, and lack such a grasping structure.

***Rhopalaemon belindae* (Kemp, 1925) new combination**

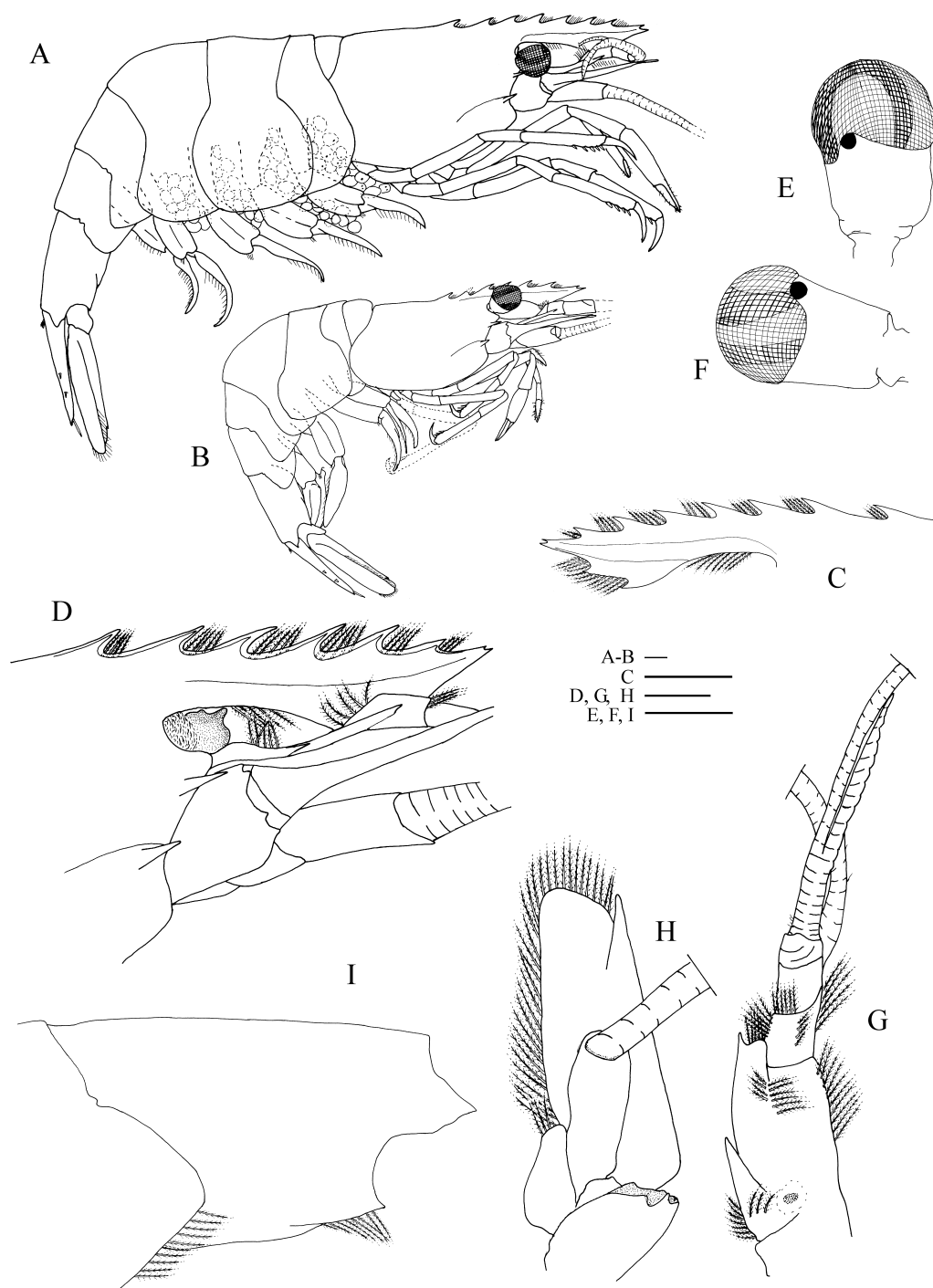
*Leander belindae* Kemp, 1925: 308–311, fig. 12, 13a–e. – Kurien, 1954: 71.

*Palaemon (Palaemon) belindae*. – Holthuis, 1950: 7. – Ravindranath, 1979: 189–191  
figs. 1a–c. – Pereira, 1997: 50.

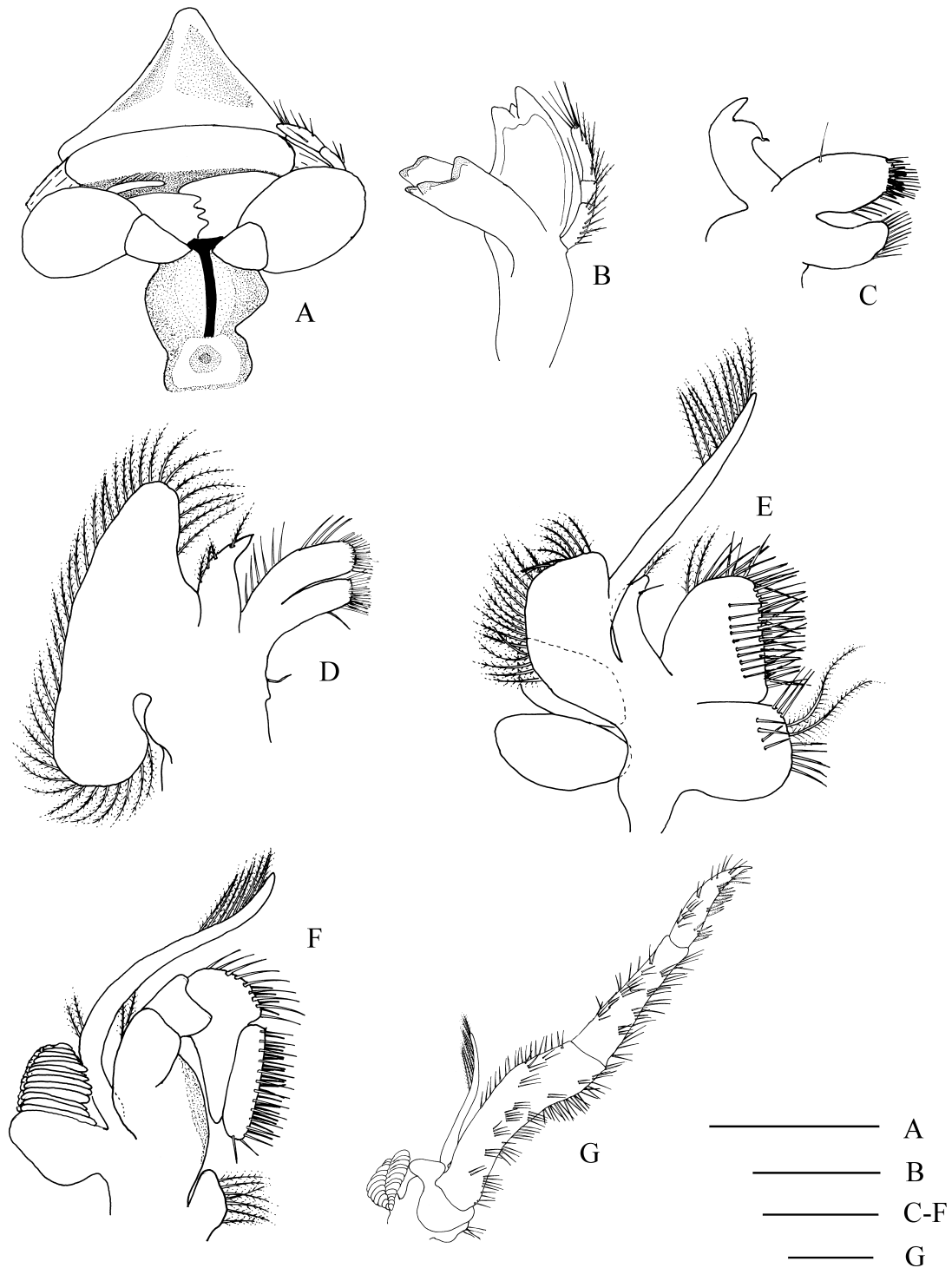
*Palaemon belindae*. – Dutt & Ravindranath, 1973: 124. – Jayachandran, 2001: 209,  
figs. 56a–e.

**Material examined. Syntypes:** (i) 1 ♂, pocl 5.9 mm; 1 ov. ♀, pocl 8.5 mm; Kilakarai, Ramnad District, Gulf of Mannar, S. India; 18.II.1913; leg. S.W. Kemp; RMNH.D.7691. (ii) 4 ov. ♀♀, pocl 7.9–9.1 mm; 1 ♀, pocl 6.6 mm; rockpools, Kilakarai, Gulf of Mannar, S. India; coll. Zoological Survey of India; NHM 1924.1.25.17–21. **Non-type material:** (i) 3 ov. ♀♀, pocl 7.6–9.7 mm; 3 ♀♀ pocl 3.3–6.4 mm; 2 ♂♂, pocl 4.0–4.9 mm; 1 individual, pocl 2.2 mm; amongst rocky blocks, Waltair Beach, Andhra Pradesh, India; 07.III.1980; leg. P. Noël; MNHN 8141. (ii) 6 ov. ♀♀, pocl 7.4–9.9 mm; 1 ♀, pocl 6.9 mm; 2 ♂♂, pocl 5.3–5.5 mm; amongst rocky blocks, Waltair Beach, Andhra Pradesh, India; 05.III.1980; leg. P. Noël; MNHN 8137.

**Description.** Carapace glabrous (Figures 1A, B). Rostrum (Figures 1C, D) slightly descendant with strong lateral ridge; much shorter than carapace, reaching to base of distolateral tooth of scaphocerite; armed with 7–8 strong dorsal teeth and 2 ventral teeth; dorsal teeth without weakly constricted bases, posterior 2–3 teeth situated behind orbit, proximal-most situated at about one third carapace length; spacing between teeth roughly equal; tip of rostrum either simple pointed or bifid; double row of setae present in ventral unarmed portion, strong, single row of setae present between teeth both dorsally and ventrally. Antennal and branchiostegal teeth (Figure 1D) present, subequal in size, sub-marginal. Anterior margin of carapace distinctly concave in region of branchiostegal tooth. Branchiostegal groove originating dorsal to branchiostegal tooth, trending downwards, finishing at about one third carapace length, slightly lower than at its origin. Sub-orbital lobe produced, angular (Figure 1D); pterygostomial angle rounded. Béc ocellaire (Figure 1D) globular with slightly concave anterior margin, pronounced, slightly hooked median process, directed upwards at about a 45° angle, dorsal surface with strong concavity.



**Figure 1.** *Rhopalaemon belindae* comb. nov.: A, Habitus, lateral view, female syntype; B, same, male syntype; C, rostrum, left lateral view; D, carapace anterior portion, right lateral view; E, left eye, dorsal view; F, same, lateral view; G, left antennular peduncle, dorsal view; H, left scaphocerite, ventral view; I, posterior portion of abdomen, left lateral. A–B (RMNH D 7691 male, pochl. 5.9 mm, female, pochl. 8.5 mm); C–I (ov. female, pochl. 8.1 mm, MNHN 8137). All scale bars indicate 1.0 mm.



**Figure 2.** *Rhopalaemon belindae* comb. nov., MNHN 8137: A, paragnaths and epistome, ventral view; B, left mandible, mesial view; C, maxillula, ventral view; D, maxilla, ventral view; E, first maxilliped, ventral view; F, second maxilliped, ventral view; G, third maxilliped, mesial view. A (ov. female, pochl. 8.1 mm); B–G (ov. female, pochl. 9.7 mm). All scale bars indicate 1.0 mm.

Eye (Figures 1E, F) well developed, with pigmented cornea; two concentric bands of pigment present on cornea, lower band usually faint; cornea slightly wider than stalk, approximately equal in length; ocellus present on dorsomedial side.

Antennular peduncle (Figure 1G) extending almost to distal margin of scaphocerite; basal segment 1.7 times as long as wide, slightly convex outer margin, stylocerite acute; distolateral tooth far exceeding laminar portion, extending to almost level with distal margin of penultimate segment; ventro-medial tooth present; statocyst with statolith; ultimate segment 1.6 times as long as penultimate, combined length slightly less than 0.7 times that of basal segment.

Dorsal flagellum of antennula fused for one quarter of length (approximately 8 segments fused, 28 free); free portion strongly serrate on ventral margin, with several aesthetascs on each segment.

Scaphocerite (Figure 1H) broad, laminar, 2.6 times as long as broad; outer margin straight, terminating in a tooth, falling short of distal margin of lamina; basal segment of antenna with reduced lateral tooth. Flagellum of antenna slightly longer than length of body.

Abdominal pleura furnished with plumose setae on ventral margin (Figure 1I); fifth pleuron posterodistal angle evenly rounded; sixth segment approximately 1.4 times length of fifth; posterolateral margin angular, without notch disto-ventrally; median lobe acute, with rounded ventral submedian process.

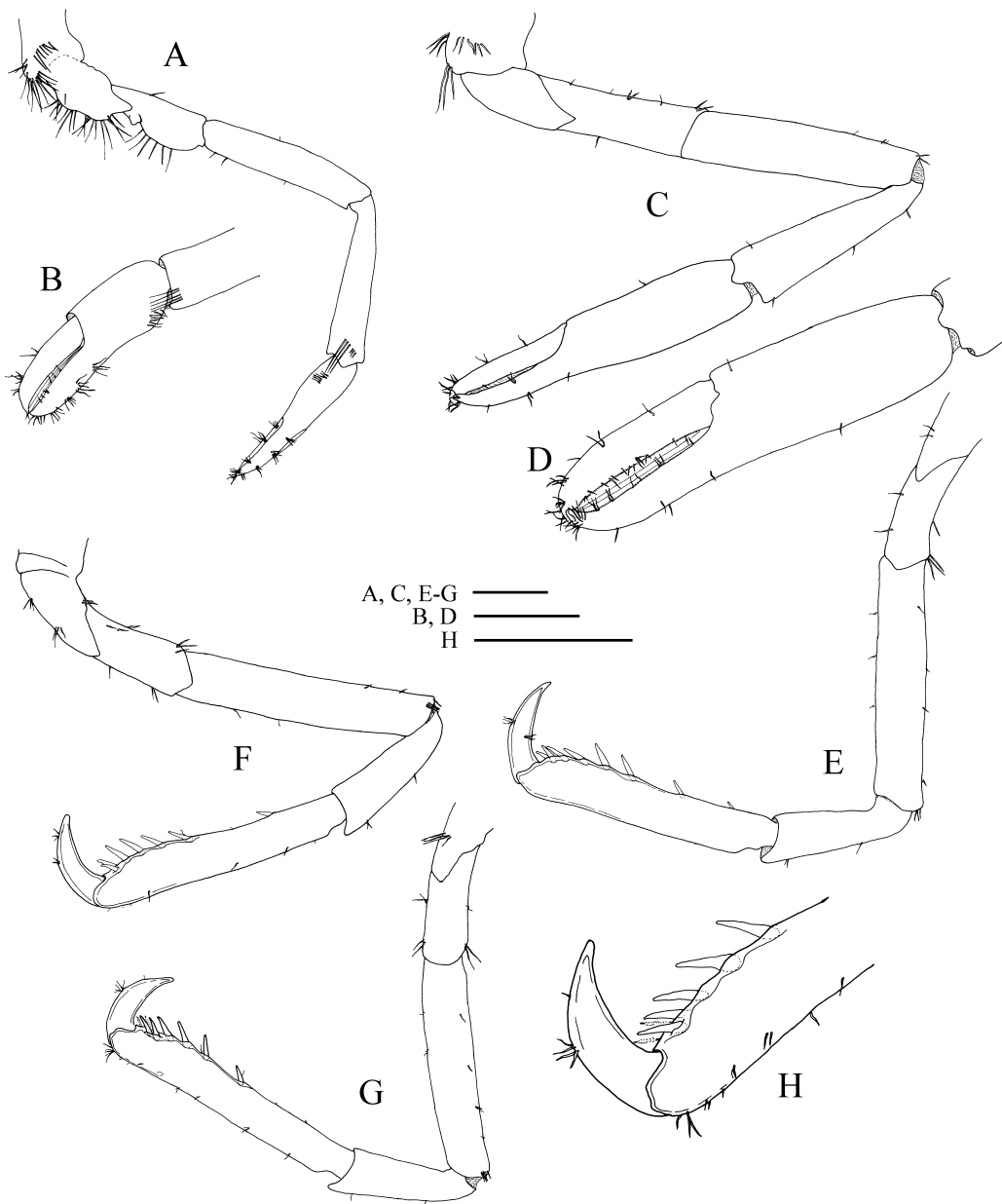
Thoracic sternal armature sexually dimorphic. Fourth thoracic sternite of females (Figure 4H) armed with sharp median tooth with strong, incomplete posterior ridge; fifth thoracic sternite with incomplete ridge; sixth and seventh with low rounded median bosses only; eighth sternite with small blunt median tubercle; in ovigerous and post-ovigerous females eighth sternite with flattened setose plate. Fourth thoracic sternite of males (Figure 4I) as in females; fifth to seventh thoracic sternites with low, rounded median bosses; eighth sternite with well developed, sharp median conical tooth.

Abdominal sternal armature sexually dimorphic. First to third abdominal sternites of females with small blunt median tubercle; fourth sternite unarmed; fifth with longitudinal ridge. In males, first to third abdominal sternites bearing narrow, parallel sided, blunt tipped tooth; fourth abdominal sternite unarmed; fifth abdominal sternite as in females. Pre-anal plate (Figure 4A) armed with well developed tooth in both sexes.



Mandible (Figure 2B) with three segmented palp; basal segment twice length of second segment, terminal segment 1.2 times length of basal segment; outer margin of palp fringed with simple, pappose setae, approximately 5 simple apical setae, disto-medial margin of second segment with single, long, simple seta. Incisor process of mandible with 3 teeth on right mandible, middle one smallest, and 4 teeth on left mandible, middle 2 smaller than outer teeth; molar process with 4 teeth of varying sizes. Paragnaths (Figure 2A) covering about half mandibles; alae formed by broad, transverse broadly oval, distal lobes, ventromedial lobes triangular. Corpus short, narrowly separated medially; base with two carinae. Epistome (Figure 2A) triangular with rounded anterior angle and strong anteromedian carina. Labrum (Figure 2A) narrow, rectangular. Maxillula (Figure 2C) with lower lacinia sub-rectangular, smaller and narrower than upper lacinia, with stout setae distally; upper lacinia with several distal spines and stout setae; with single simple seta on upper margin; palp with bifid tip; upper process naked, lower process broad with setiform process on ventral tubercle. Maxilla (Figure 2D) with upper lacinia deeply cleft, ending in several stout, plumose setae, several simple setae on upper margin; palp well developed, broad with few plumose setae on outer margin; scaphognathite large, fringed with plumose setae. First maxilliped (Figure 2E) with endites separated by distinct notch; palp slender, slightly twisted, with single subterminal simple seta and terminal plumose seta; exopod well developed, slender, furnished with plumose setae distally; caridean lobe well developed, broad, fringed with plumose setae; epipod large, bilobed, lobes sub-rectangular. Second maxilliped (Figure 2F) with broad rectangular ultimate segment; penultimate segment broadly triangular, with convex, semicircular upper margin; exopod much longer than endopod; epipod and well developed podobranch present. Third maxilliped (Figure 2G) pediform; ultimate segment 0.75 times length of penultimate; ischiomerus broadening distally, with strongly curved dorsal margin; exopod 0.7 times length of ischiomerus; epipodal plate broadly ovate; two arthrobranches present, one rudimentary and obscured by larger.

Well developed pleurobranches present on all thoracic legs. First pereopod (Figure 3A) overreaching scaphocerite by length of fingers; basis approximately 0.6 times length of ischium; ischium disto-ventrally expanded; merus 1.3 times length of ischium; carpus 1.9 times as long as merus and slightly expanded distally; chela (Figure 3B) 0.8 times length of carpus, fingers equal to palm, with tufts of setae; carpal-propodal brush present. Second pereopod (Figure 3C) extending beyond



**Figure 3.** *Rhopalaemon belindae* comb. nov., ovigerous female, pochl. 8.1 mm MNHN 8137: A, first pereopod, mesial view, chela rotated; B, same, chela; C, second pereopod, mesial view, chela slightly rotated; D, same, chela; E, third pereopod, mesial view; F, fourth pereopod, mesial view; G, fifth pereopod, mesial view; H, same, distal part. All scale bars indicate 1.0 mm.

scaphocerite by half length of palm of chela; ischium 3.5 times length of basis; merus 1.3 times length of ischium; carpus 0.75 times length of merus, strongly expanded distally; chela (Figure 3D) about 1.7 times length of carpus; fingers approximately 0.4 times length of chela, 0.7 times length of palm, cutting edges covered with stout setae, proximally without dentition. Ambulatory pereopods robust, broadly similar in length. Third pereopod (Figure 3E) overreaching scaphocerite by length of dactylus; ischium 2.1 times length of basis; merus twice length of ischium; carpus 0.5 times length of merus, equal in length to ischium; propodus 2.0 times length of carpus, equal in length to merus, distally dilated, 1.3 times wider distally than proximally, ventral margin of dilated portion armed with 4 single spines and a distal pair, a further spine occasionally present further along margin; dactylus, stout, simple, strongly curved, about 0.3 times length of propodus. Fourth pereopod (Figure 3F) reaching end of scaphocerite; ischium 2.3 times length of basis; merus 2.4 times length of ischium; carpus 0.5 times length of merus, slightly longer than ischium; propodus slightly less than 2.0 times length of carpus, distally dilated, 1.3 times wider distally than proximally, ventral margin of dilated portion armed with 4 single spines and a distal pair, a further spine occasionally present further along margin; dactylus stout, simple, strongly curved, about 0.3 times length of propodus. Fifth pereopod (Figure 3G) falling short of distolateral tooth of scaphocerite by length of dactylus; ischium 2.0 times length of basis; merus 2.4 times length of ischium; carpus 0.5 times length of merus; propodus 2.1 times length of carpus, distally dilated, 1.3 times wider distally than proximally, ventral margin of dilated portion armed with 4–5 single spines and a distal pair, a further spine occasionally present further along margin, grooming brush (Figure 3H) comprises 1 poorly developed row of serrulate setae hidden between ultimate and penultimate spines; dactylus stout, simple, strongly curved, about 0.35 times length of propodus.

First pleopod sexually dimorphic in proportions, lacking appendix interna in both sexes; in males endopod 0.5–0.6 times length of exopod, both exo- and endopods fringed with plumose setae but medial portion of inner margin of endopod devoid of plumose setae, with 7 spines (Figure 4B); in females, endopod approximately 0.4 times length of exopod. Second to fifth pleopods broadly similar with endopod being slightly shorter than exopod, bearing appendix interna. Second pleopod of males with appendix masculina; about 1.4 times length of appendix interna (Figure 4C), furnished with 8 lateral and 3 apical simple setae.

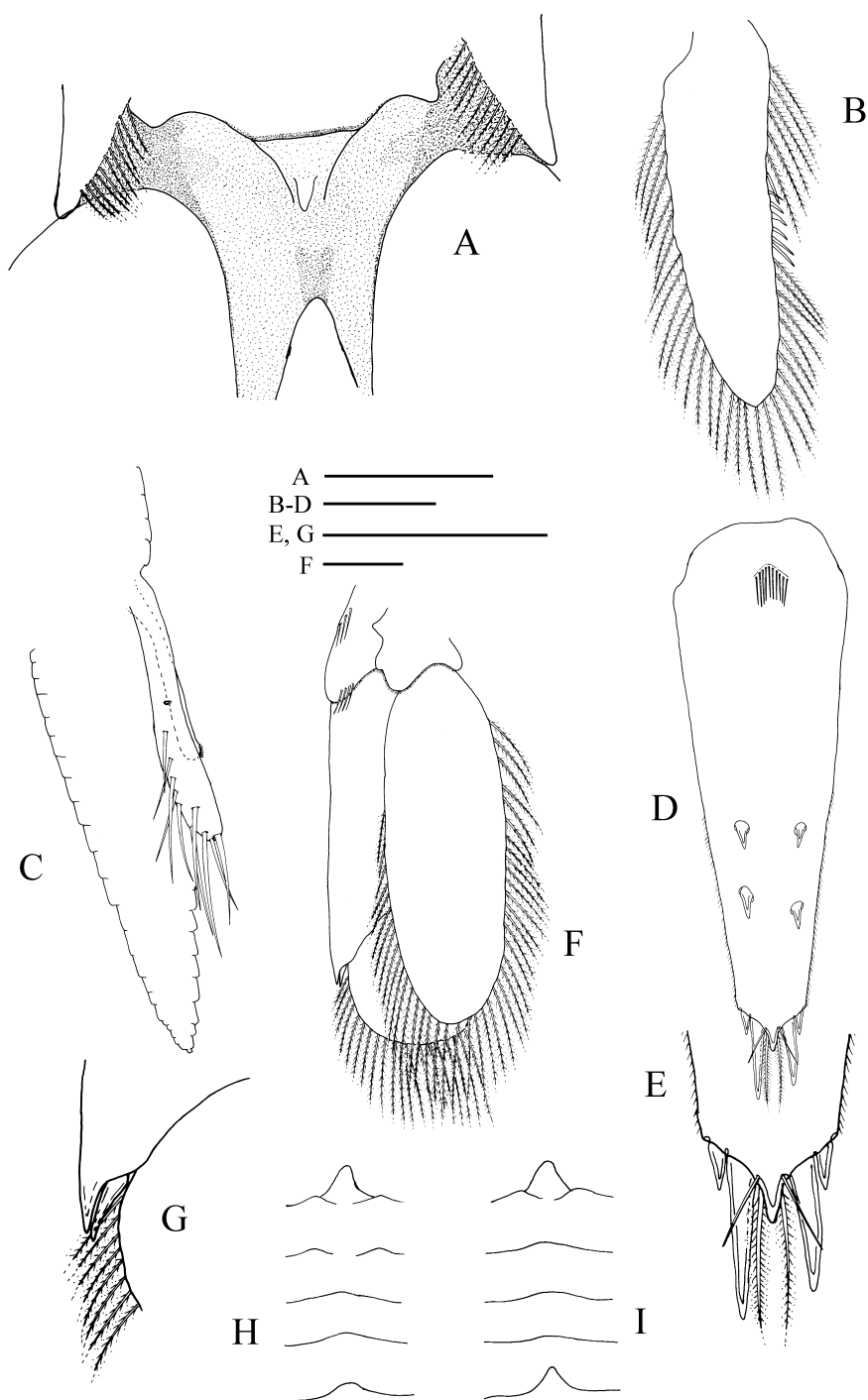


Figure 4. *Rhopalaemon belindae* comb. nov., MNHN 8137: A, pre-anal plate, ventral view; B, endopod of first pleopod of male, anterior view; C, appendix interna and appendix masculina, anterior view; D, telson, dorsal view; E, same, distal; F, uropods, dorsal view; G, same, close up of lateral tooth and spine; H, thoracic sternal armature, female; I, same, male. A, D–F (ov. female, pochl. 8.1 mm); H (female, pochl. 6.9 mm); B–C, I (male, pochl. 5.5 mm). All scale bars indicate 1.0 mm, H–I not to scale.

Telson (Figure 4D) 1.1 times length of sixth pleonite; length:width ratio 3:1 proximally narrowing to 7.8:1 distally; dorsal surface with 2 pairs of spines and 1 pair of simple setae subdistally on median process; proximal dorsal tuft of about 10 simple setae present; proximal pair of spines situated at about 0.55 of telson length, distal pair at about 0.7–0.75 length; marginal setae present in distal half only; posterior margin (Figure 4E) prolonged into acute process, with 1 pair of submedian plumose setae and 2 pairs of spines, inner pair about 3 times longer than outer pair; median process exceeding outer pair of spines.

Uropods (Figure 4F) broadly ovate, overreaching telson by 0.3 times length of endopod; exopod slightly longer than endopod, weak diarthrosis present; mobile lateral spine of exopod overreaching fixed tooth by length of tip (Figure 4G).

Eggs 0.7x0.6 mm.

**Colour pattern.** According to Kemp (1925: 311): “Translucent, thinly speckled with yellow and dark green chromatophores and with a certain amount of scattered white pigmentation in the middle of the carapace. On the dorsal side of the abdomen at the hinder end of the second and third somites there was a lenticular patch of pale dull pink and the distal two thirds of the tail-fan were heavily spotted with dark green or yellow brown. All the legs were banded with blue and each also bore a light red patch at the distal end of the merus, carpus and propodus or palm. The eggs were dark grey or olive. Young specimens were always paler than adults.” Additionally, Kemp (1925: 309) noted: “there are two concentric rings of dark pigment on the cornea, but the lower one is usually faint”, whilst Ravindranath (1979: 190) remarked: “antennular flagellae bear dark (greenish-maroon) and pale (pink) alternating bands”.

**Distribution and habitat.** Currently known from two locations in the southern Indian state of Tamil Nadu (Keelakarai, Kanyakumari), as well as Andhra Pradesh State (Visakhapatnam), from littoral pools.

### Acknowledgements

Charles Fransen and Jacques Smit (Naturalis), Miranda Lowe (NHM) and Regis Cleva (MNHN) are thanked for the loan of specimens of this rarely collected species. Magnus Johnson (University of Hull) provided comments on an earlier draft of the manuscript that improved the quality of the final paper. The study was partially supported by Unicmarine Ltd.

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**Marine and estuarine shrimp fauna of Taiwan (Crustacea: Decapoda):  
Subfamily Palaemoninae**

**Abstract**

The marine and estuarine Palaemoninae fauna of Taiwan is assessed based on museum and fresh collections as well as reports in the literature. A total of thirteen species belonging to seven genera are reported, of which four have not been previously reported for the fauna of Taiwan.

**Introduction**

Palaemoninae are one of the most speciose shrimp taxa and often numerically dominant where they occur. They are widespread in tropical and temperate regions, with representatives in fresh, brackish, marine and subterranean waters. Unlike the Pontoniinae, which contains a large number of morphologically diverse, commensal species, the Palaemoninae are all free living and have a fairly conservative morphology. The subfamily contains many of the larger, better known and commercially important ‘prawn’ species. Currently, 21 genera are recognised within the subfamily with more than 370 species (De Grave et al., 2009; Ashelby & De Grave, 2010; Wowor & Ng, 2010), of which, eight have been previously recorded from Taiwan. Here the marine and estuarine Palaemoninae fauna of Taiwan is reappraised based on fresh material as well as museum collections and literature records. The genus *Macrobrachium* Spence Bate, 1868 is not considered in the present study, as the majority are freshwater species, although some can be found in brackish water. Taiwanese species of this genus have been covered by Shy and Yu (1998), Lin (2007) and Chen et al. (2009), with 21 species known. The genus is included in the key to genera to facilitate its recognition when encountered in brackish waters.

Rostral formulae are given as subapical teeth + dorsal series/ventral teeth except for *Urocaridella* where they are given as subapical teeth + dorsal series + basal teeth/ventral teeth. Post-orbital carapace length (pocl., in mm) is used as the standard measurement. The following institutional abbreviations are used NTOU (National

Taiwan Ocean University), OUMNH-ZC (Oxford University Museum of Natural History Zoological Collection).

### **Subfamily Palaemoninae Rafinesque, 1815**

**Type genus.** — *Palaemon* Weber, 1795.

**Diagnosis.** — Telson usually armed with 2 pairs of posterior spines (often 3 pairs in *Coutierella*) and 2 or more submedian setae; third maxilliped usually with 2 arthrobranches.

#### **Key to the genera of Palaemoninae from Taiwan**

1. Carapace with branchiostegal spine, sometimes arising slightly posterior to margin ..... **2**
  - Carapace with spine clearly in hepatic position..... **7**
2. Carapace with well developed branchiostegal suture ..... **3**
  - Branchiostegal suture absent ..... **4**
3. Basal portion of rostrum with strongly elevated crest ..... *Exopalaemon*
  - Basal portion of rostrum without elevated crest ..... *Palaemon*
4. Dactylus of fourth and fifth pereopods greatly elongated, longer than combined length of propodus and carpus; rostrum with strong basal crest; strong tooth on dorsal surface of stylocerite; endopod of first pleopod of males without marginal appendix..... *Nematopalaemon*
  - Dactylus of the fourth and fifth pereopods shorter than propodus; basal crest of rostrum weak or absent; stylocerite without dorsal tooth; endopod of 1<sup>st</sup> pleopod of males with marginal appendix ..... **5**
5. Rostrum at most slightly upturned, all dorsal rostral teeth of similar size and not serrate on concave margin, no epigastral tooth ..... **6**

- Rostrum strongly upturned distally, bearing two strong basal teeth, clearly larger than remaining dorsal rostral teeth, with minute serrations on concave margin, a further strong tooth is present in epigastral region of carapace. .... *Urocaridella*
- 6. Mandible with palp ..... *Leander*
- Mandible without palp ..... *Leandrites*
- 7. Dactyli of third to fifth pereopods biunguiculate; marine ..... *Brachycarpus*
- Dactyli of third to fifth pereopods simple; usually freshwater ..... *Macrobrachium*

### ***Brachycarpus* Spence Bate, 1888**

*Brachycarpus* Spence Bate, 1888: 795. [type species *Brachycarpus savignyi* Spence Bate, 1888 (junior subjective synonym of *Brachycarpus biunguiculatus* Lucas, 1846), by original designation. Gender: masculine. Name placed on the Official List of Generic Names in Zoology in Opinion 470 in 1957]

**Diagnosis.** — Rostrum well developed, compressed and provided with teeth; carapace with antennal and hepatic spines, without branchiostegal groove; telson with two pairs of dorsal and two pairs of posterior spines, posterior margin also with several hairs; cornea of eyes well developed and pigmented; mandible with 3 segmented palp; all maxillipeds with exopods; pleurobranchs on third maxilliped and all pereopods; dactyli of ambulatory pereopods biunguiculate; propodus of the fifth with only single row of setae in grooming brush; first pleopod of males with appendix interna.

**Remarks.** — Three species of *Brachycarpus* are currently known: *B. holthuisi* Fausto Filo, 1966, from Brazil, *B. crosnieri* Bruce, 1998, from a number of locations in the Indo-West Pacific, and *B. biunguiculatus*, from shallow tropical waters worldwide. The genus is unique within the subfamily in having biunguiculate dactyli on the ambulatory pereopods.

***Brachycarpus biunguiculatus* (Lucas, 1846)**

*Palaemon biunguiculatus* Lucas, 1846: 45; plate 4, figs. 4-4a. [type locality: Algeria]

*Brachycarpus savignyi* Spence Bate, 1888: 795; plate 124, fig. 4. [type locality: Bermuda]

*Brachycarpus neapolitanus* Cano, 1890: 38; plate 4, fig. 1. [type locality: Gulf of Naples]

*Palaemonella rathbunensis* Borradaile, 1917: 358. [type locality: Hawaiian Islands]

*Brachycarpus biunguiculatus*.—Holthuis, 1952a: 3, plate 1, figs. a-q.

**Material examined.** — Magang, Taipei County; 04.09.1994; 1 ♀, pochl. 3.9 mm; NTOU.

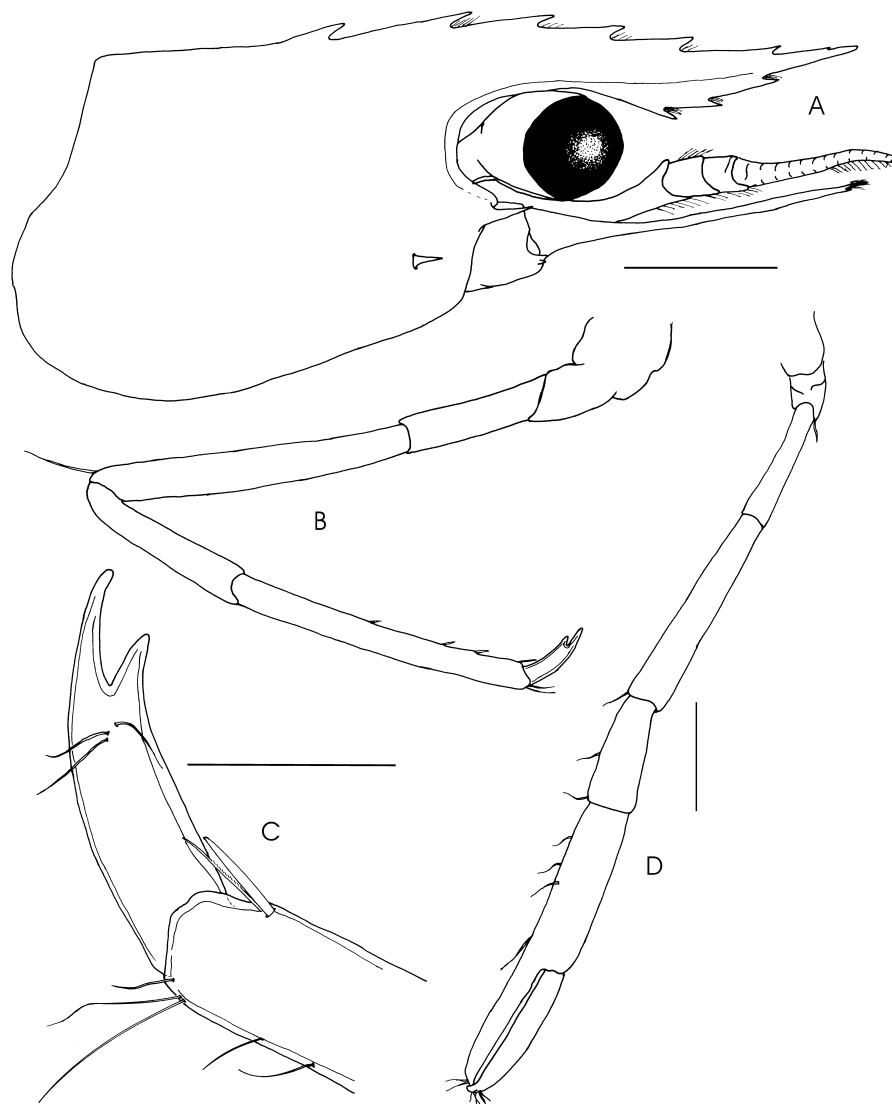
**Diagnosis.** — Rostrum nearly straight dorsally; dorsal spines of telson not submarginal, directed posteriorly; anterolateral tooth of basal segment of antennular peduncle overreaching second segment; mandibular palp not reduced, reaching at least to distal third of incisor process; carpus of first pereopod slightly longer than chela.

**Size.** — Maximal total length about 65 mm (Holthuis, 1952a)

**Colouration.** — The general coloration of the body is a bright orange-brown which is most marked on the abdomen, where it forms transverse bars posteriorly across each segment, and the caudal fan. The post-rostral carina is a darker rusty red but the distal part of the rostrum is nearly colourless. The antennal peduncles are pale but the flagella are reddish brown. The chela of the second pereopod has the palm orange-brown and a dark brown bar extends across the bases of the fingers, the tips of which are darker brown. The intermediate zone consists of a broad proximal band of yellow and a broad distal band of white separated by a narrower band of dark orange brown. The carpus is orange-brown with greenish distal margins. The merus is banded broadly with orange-red separated by narrow paler bands and the ischium is pale distally with the proximal half orange-red. The third to fifth pereopods are a similar orange-brown.

**Habitat.** — Littoral and sublittoral to about 56 m. In reefs and coral rubble, weed covered rocks and rock crevices, occasionally in seagrass. Primarily nocturnal, usually concealed during daylight.

**Distribution.** — Probably pantropical and subtropical.



**Figure 1.** *Brachycarpus biunguiculatus* (Lucas, 1846): Female (pocl. 3.9 mm); Magang, Taipei County; NTOU. A. carapace, right lateral view; B. left fifth pereiopod, lateral view; C. same, dactylus, mesial view; D. left second pereiopod, lateral view. Scale bars indicate 1.0 mm.

**Remarks.** — Although small and missing several pereopods, the specimen examined here undoubtedly belongs to *B. biunguiculatus* based on the proportion of the carpus of the second pereopod, the biunguiculate dactyli of the ambulatory pereopods and possession of an hepatic rather than a branchiostegal spine. This is the first record of this wide ranging species from Taiwan. A number of differing colour patterns have been described for *B. biunguiculatus* although no corresponding morphological differences having been reported. The specimen reported here was not photographed and the colour pattern described above is taken from the description by Bruce (1966) based on material from Latham Island, Tanzania.

### *Exopalaemon* Holthuis, 1950

*Exopalaemon* Holthuis, 1950: 45. [type species *Palaemon styliferus* H.Milne Edwards, 1840, by original designation. Gender: masculine]

**Diagnosis.** — Rostrum with elevated dentate basal crest; carapace with branchiostegal spine and branchiostegal suture, without hepatic spine; mandible with palp; third to fifth pereopods with dactyli simple, not biunguiculate, shorter than propodus; propodus of fifth pereopod with well developed grooming brush; endopod of first pleopod of male without appendix interna.

**Remarks.** — Of the ten known species of *Exopalaemon*, two are recorded from Taiwan. *Exopalaemon* is characterised by having a strong basal crest to its rostrum, a feature it shares with *Nematopalaemon*. Although primarily a freshwater species, *E. modestus* is included for completeness.

Chace and Bruce (1993) stated that *Exopalaemon* lacks a tooth on the fourth thoracic sternite, however such a tooth is present in the specimens examined here (see also remarks under *Leander*).

### Key to species *Exopalaemon* from Taiwan

1. Rostrum long, distinctly longer than carapace, elevated basal crest shorter than slender distal part, with subapical tooth..... *Exopalaemon orientis*
- Rostrum short, as long as or shorter than carapace, elevated basal crest longer than slender distal part, without subapical tooth .... *Exopalaemon modestus*

*Exopalaemon modestus* (Heller, 1862)

*Leander modestus* Heller, 1862a: 527. [type locality: Shanghai, China]

*Leander macrogenitus* Yu, 1930b: 559; figs. 1a-c. [Hangchow]

*Leander modestus*.—Uéno, 1935: 274, figs. 3a-e, 4a, b.

*Palaemon (Exopalaemon) modestus*.—Holthuis, 1950: 51, fig. 10.

*Exopalaemon modestus*.—Shy & Yu, 1998: 13.—Lin, 2007: 134.—Li et al., 2007: 61, figs. 17a-k.

**Material examined.** — No Taiwanese material was available for examination.

**Diagnosis.** — Rostrum with slender distal portion almost horizontal, without subapical tooth; rostral formula 7-10/2-4; third to sixth abdominal somites not carinate in dorsal midline; mandible with 3-segmented palp; first pereopods chela slightly less than half length of carpus; second pereopods with carpus about equal to chela; third pereopods with dactyl slightly shorter (about 0.9) than propodus; fifth pereopods with dactyl less than half as long as propodus.

**Size.** — Carapace length 13.5 mm (Guo et al., 2005), maximum total length 60 mm (Holthuis, 1980).

**Colouration.** — Translucent with sparsely scattered minute red chromatophores, not forming a definite pattern.

**Habitat.** — Freshwater, between weeds or occasionally over muddy bottoms, to about 8 m. Emmett et al. (2002) report collections as deep as 26 m.

**Distribution.** — Vladivostok southwards to southern China and Taiwan. Introduced in the Columbia River on the border between Washington and Oregon, western U.S.A. (Emmett et al., 2002). Previously recorded from Taiwan by Uéno (1935), Holthuis (1950), Shy and Yu (1998) and Lin (2007).

**Remarks.** — Uéno (1935) noted a number of differences between his Taiwanese specimens and typical *E. modestus* based on Kemp's (1917) description of the species. The distal portion of the rostrum was noted as being shorter and the proportions of some of the segments of the pereopods were noted as different to the specimen described by Kemp (1917). Uéno (1935) refrained from assigning them to a new species until a greater series of material was examined. Holthuis' (1950) ovigerous female specimen was in agreement with the characters noted by Uéno

(1935) but he considered the differences so minor that they did not warrant specific status and probably resulted from age related or ecological factors.

***Exopalaemon orientis* (Holthuis, 1950)**

*Palaemon* (*Exopalaemon*) *orientis* Holthuis, 1950: 49. [replacement name for *Leander longirostris* var. *japonicus* Ortmann, 1890]

*Leander longirostris* var. *japonicus* Ortmann, 1890: 519; plate 37, figs. 14, 14z. [type locality: Tokyo Bay, Japan]

*Leander japonicus*.—Parisi, 1919: 77. plate VI, fig. 10.

*Palaemon* (*Exopalaemon*) *orientis*.—Chan and Yu, 1985: 124, text figs. 5a-e.

*Exopalaemon orientis*.—Li et al., 2007: 64, figs. 18a-h.

**Material examined.** — Fengshanxi, Hsinchu County; 07.10.1997; 1 ♂, pochl. 6.4 mm; NTOU. Donggang, Pingtung County; aquaculture ponds; approx. 22°27'19.9"N 120°28'20.4"E; 28/07/2009; 6 ♂♂, pochl. 6.8-9.0 mm; 36 ♀♀, pochl. 7.3-13.0 mm; 9 ovigerous ♀♀, pochl. 8.8-12.4 mm; OUMNH-ZC 2010-02-0078.

**Diagnosis.** — Rostrum with slender distal portion unarmed dorsally except for subapical tooth and strongly upturned; rostral formula 1+5-7/5-7; third to sixth abdominal somites not carinate in dorsal midline; mandible with 3-segmented palp; first pereopods chela about 0.75 times length of carpus; second pereopods with carpus 0.6 times as long as chela; third pereopods with dactyl about 0.75 times as long as propodus; fifth pereopods with dactyl no more than half as long as propodus

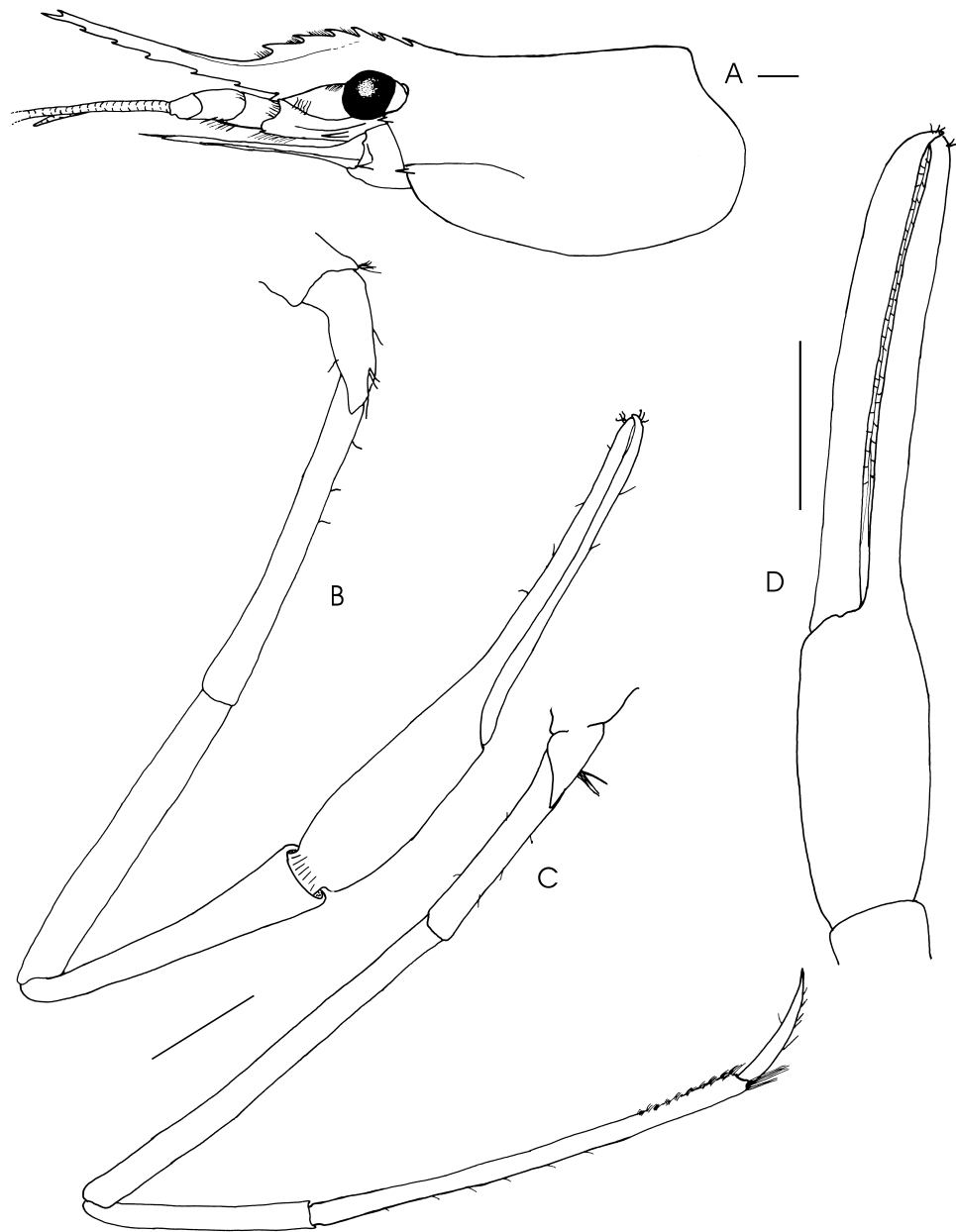
**Size.** — Carapace length 17.0 mm (Guo et al., 2005), Maximum total length of males 46 mm, of females 68 mm (Holthuis, 1980).

**Colouration.** — Body largely transparent with scattered red-brown chromatophores across carapace and abdomen, occasionally forming weak lines; antennules and distal end of rostrum are tinged blue; eggs yellow. The large blue-green patches observed in Figure 3 are thought to be a discolouration of the eggs.

**Habitat.** — Shallow marine, occasionally brackish water.

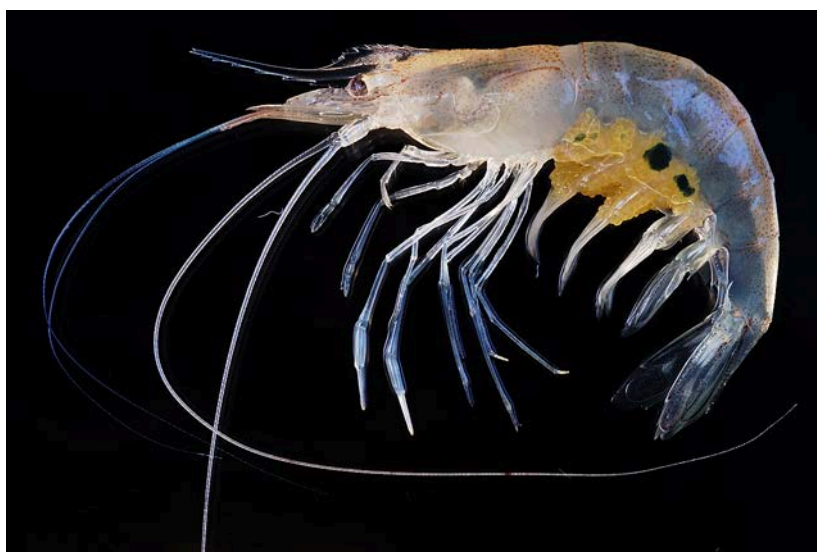
**Distribution.** — Japan to South China Sea. Previously recorded from Taiwan by Maki and Tsuchiya (1923) and at the following locations: Tamsui (Parisi, 1919), Takao [now Kaohsiung] (Balss, 1914), Donggang, Ping-Tong County (Chan & Yu, 1985).





**Figure 2.** *Exopalaemon orientis* (Holthuis, 1950): Male (pocl. 7.8 mm), Donggang, Pingtung County; OUMNH-ZC 2010-02-0078. A. carapace, left lateral view; B. right second pereopod, mesial view; C. right fifth pereopod, mesial view; D. right second pereopod chela, mesial view. Scale bars indicate 1.0 mm.

**Remarks.** — Although widely reported in the literature, *E. orientis* is poorly known and Holthuis (1950) suggested that a good description of the species is sorely needed. Despite this suggestion, more than half a century later, no description has been produced. Such a redescription is beyond the scope of this study and would require examination of far more material from across the range of this species than has been examined here but Holthuis' suggestion remains valid. *Exopalaemon orientis* is undoubtedly closely related to *E. carinicauda* Holthuis, 1950 but differs from that species by having a smooth rather than carinate abdomen, lacking a groove on the



**Figure 3.** *Exopalaemon orientis* (Holthuis, 1950): Ovigerous female, Donggang, Pingtung County; OUMNH-ZC 2010-02-0078. Photo by T.-Y. Chan.

dorsal side of the palm of the chela of the second pereiopod and in the proportions of the segments of the pereiopods. The Taiwanese material examined agrees with available diagnoses and figures for *E. orientis* in Li et al. (2004) and Li et al. (2007) although they are very much smaller than the quoted maximum size for the species, despite being sexually mature.

*Exopalaemon orientis* was listed as a pest species in aquaculture ponds by Chan and Yu (1985).

***Leander* Desmarest, 1849**

*Leander* Desmarest, 1849 [type species *Leander erraticus* Desmarest, 1849 (junior subjective synonym of *Palaemon tenuicornis* Say, 1818), by original designation and monotypy. Gender: masculine. Name placed on the Official List of Generic Names in Zoology in Opinion 564 in 1959)

**Diagnosis.** — Rostrum without elevated basal crest; carapace with submarginal branchiostegal spine, without hepatic spine or branchiostegal suture; mandible with palp; third to fifth pereopods with dactyli simple, not biunguiculate, shorter than propodus; propodus of fifth pereopod without grooming brush; endopod of male 1st pleopod with appendix interna, except in *L. manningi*.

**Remarks.** — Chace and Bruce (1993) regarded the absence of a conical tooth on the fourth thoracic sternum a valuable generic character within the Palaemoninae and to distinguish this genus, similar to its use in differentiating Pontoniinae genera. When describing *Leander manningi* Bruce, 2002 Bruce (2002) noted that this species possessed a sternal tooth on this segment and suggested that this may also be present in *L. paulensis* Ortmann, 1897 and thus amended the generic diagnosis for *Leander*. Examination of this character in the present specimens of *L. tenuicornis* shows that a well developed tooth is present in all specimens. Comparison with other material of *L. tenuicornis* from elsewhere in its range also shows that this tooth is present in all examined specimens. This indicates that either the character is variable within the genus or that the tooth may be difficult to discern in some specimens. In addition, Bruce (2002) noted that *L. manningi* was atypical of the genus as males did not possess an appendix interna on the first pleopod.

The genus contains five species with only the near cosmopolitan *L. tenuicornis* reported here from Taiwan.

*Leander tenuicornis* (Say, 1818)

*Palaemon tenuicornis* Say, 1818: 249. [type locality: Banks of Newfoundland]

*Leander tenuicornis*.—Holthuis, 1950: 26, figs. 1a-e, 2a-h.—Chace & Bruce, 1993: 6.—Li et al., 2007: 70, fig. 21a-h.

**Material examined.** — Keelung City fishing port, artificial lobster larvae collector; 30.12.1993; 1 ♂, pochl. 5.3 mm; NTOU. Keelung City fishing port, artificial lobster larvae collector; 15.11.1993; 4 ♂♂, pochl. 2.4-6.1 mm; NTOU.

**Diagnosis.** — Rostrum sexually dimorphic, expanded vertically in female, less than 1.5 times carapace length; rostral formula 2+6-12/5-7; basal antennular segment straight or concave distally, lateral to second segment; stylocerite reaching beyond midlength of basal antennular segment; second pereopods with carpus shorter than chela, fingers longer than palm, without teeth on opposable margin of fixed finger.

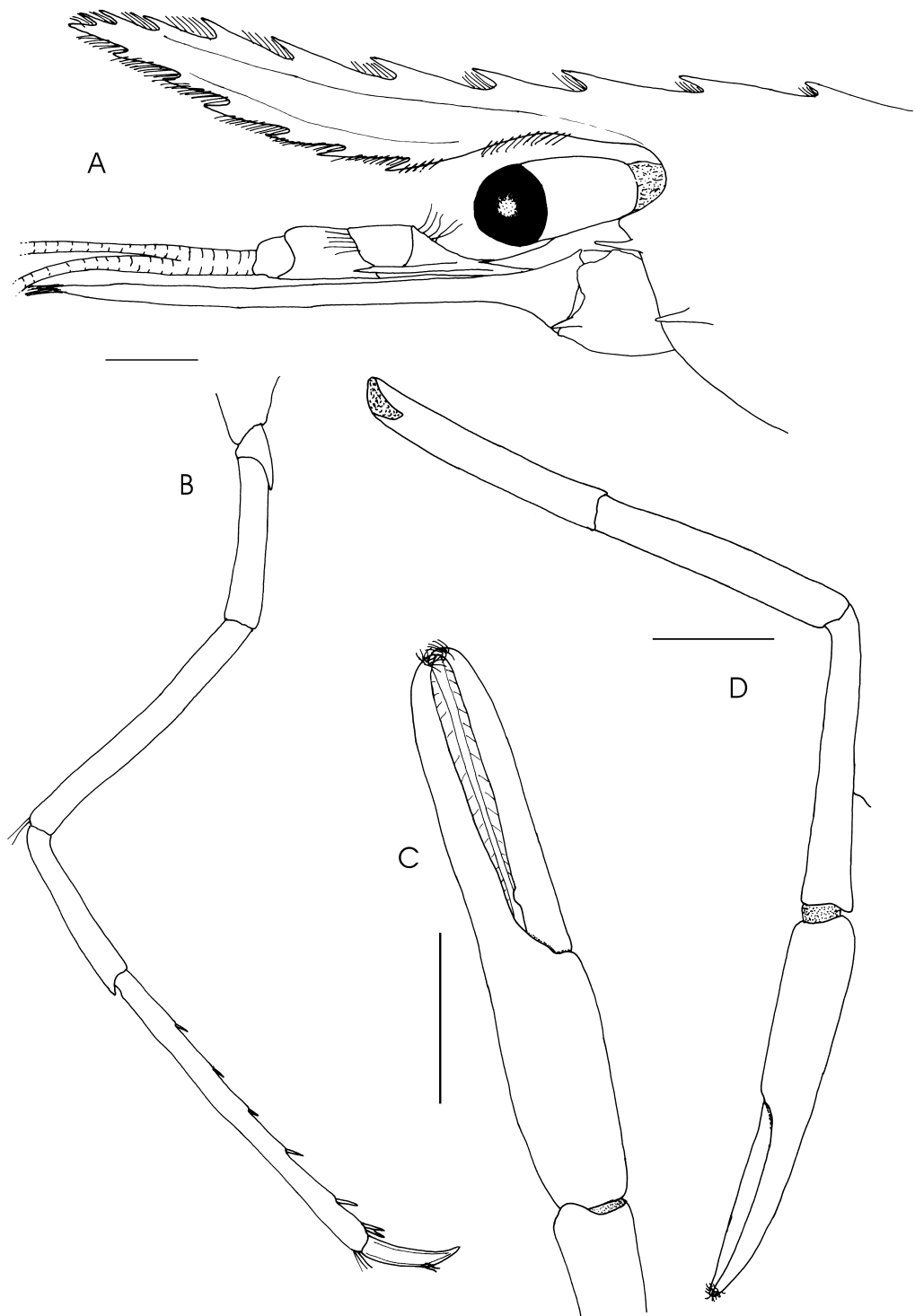
**Size.** — Maximum postorbital carapace length about 8 mm (Chace & Bruce, 1993)

**Colouration.** — Mottled green-brown and white; first and third pleurae with large ‘eye’ spot varying from purple to green-brown colour; eggs brown.

**Habitat.** — Shallow water, frequently associated with seagrass beds, algae and, in the open sea, floating mats of *Sargassum* C. Agardh, 1820.

**Distribution.** — Near cosmopolitan in tropical and subtropical seas being absent only from the eastern Pacific. As noted by Bruce (2002), a record from the Falkland Islands (Kemp, 1925) has never been verified. This is the first record of *L. tenuicornis* from Taiwan.

**Remarks.** — Although the present specimens are damaged and in poor condition there is no doubt that they belong to this widespread species. The rostrum of *L. tenuicornis* is sexually dimorphic being broadly arched in females and slightly ascendant with converging margins in males. No females were found amongst the Taiwanese material examined here but the difference in rostral shape is adequately figured by Holthuis (1950) and Li et al. (2007). As mentioned above, all specimens possessed a conical tooth on the fourth thoracic sternite, a feature previously believed to be absent in the species (Chace & Bruce, 1993).



**Figure 4.** *Leander tenuicornis* Say, 1818: Male (pocl. 5.3 mm), Keelung City; NTOU. A. carapace, anterior left lateral view; B. left fifth pereiopod, lateral view; C. left second pereiopod chela, mesial view; D. left second pereiopod, lateral view. Scale bars indicate 1.0 mm.

***Leandrites* Holthuis, 1950**

*Leandrites* Holthuis, 1950: 34. [type species *Leander celebensis* De Man, 1881 by original designation. Gender: masculine]

**Diagnosis.** — Rostrum without elevated basal crest; carapace with submarginal branchiostegal spine, without hepatic spine or branchiostegal suture; mandible without palp; third to fifth pereopods with dactyli simple, shorter than propodus; propodus of fifth pereopod without grooming brush; endopod of male first pleopod with appendix interna.

**Remarks.** — *Leandrites* differs from *Leander* solely by the absence of the mandible palp (present in *Leander*). The use of a single negative character to differentiate between genera has been questioned in the case of *Palaemon* and *Palaemonetes* by Chace (1972), which likewise differ solely by the presence or absence of the mandible palp (also see Kemp, 1925). Intraspecific variation in the number of segments of the palp and even its presence has been demonstrated in *Palaemon* (Fujino & Miyake, 1968; Chace, 1972) suggesting this may not be a good character between these genera. Carvacho (1977) documented similar variation in the number of segments of the palp of *Leander* and it is conceivable that it too may occasionally be absent from these species. A detailed study to ascertain the limits of variability in the palp of *Leander* and the validity of *Leandrites* is therefore desirable.

A key to the known species of *Leandrites* can be found in Chace and Bruce (1993). A single species of the genus is here reported from Taiwan.

***Leandrites deschampsi* (Nobili, 1903)**

*Leander Deschampsii* Nobili, 1903: 8. [type locality: Singapore]

*Leandrites deschampsi*.—Chace & Bruce, 1993: 7.—Li et al., 2007: 72, figs. 22a-j.

**Material examined.** — Kaohsiung Port, Kaohsiung City; 15.04.1996; 1 ♂, pochl. 4.9 mm; 3 ovigerous ♀♀, pochl. 5.6-6.0 mm; NTOU.

**Diagnosis.** — Rostrum upturned distally, distinctly overreaching antennal scale; rostral formula 1-2+8-12/4-6; 2nd pereopods overreaching antennal scale by length of chela and part of carpus; carpus distinctly longer than chela.

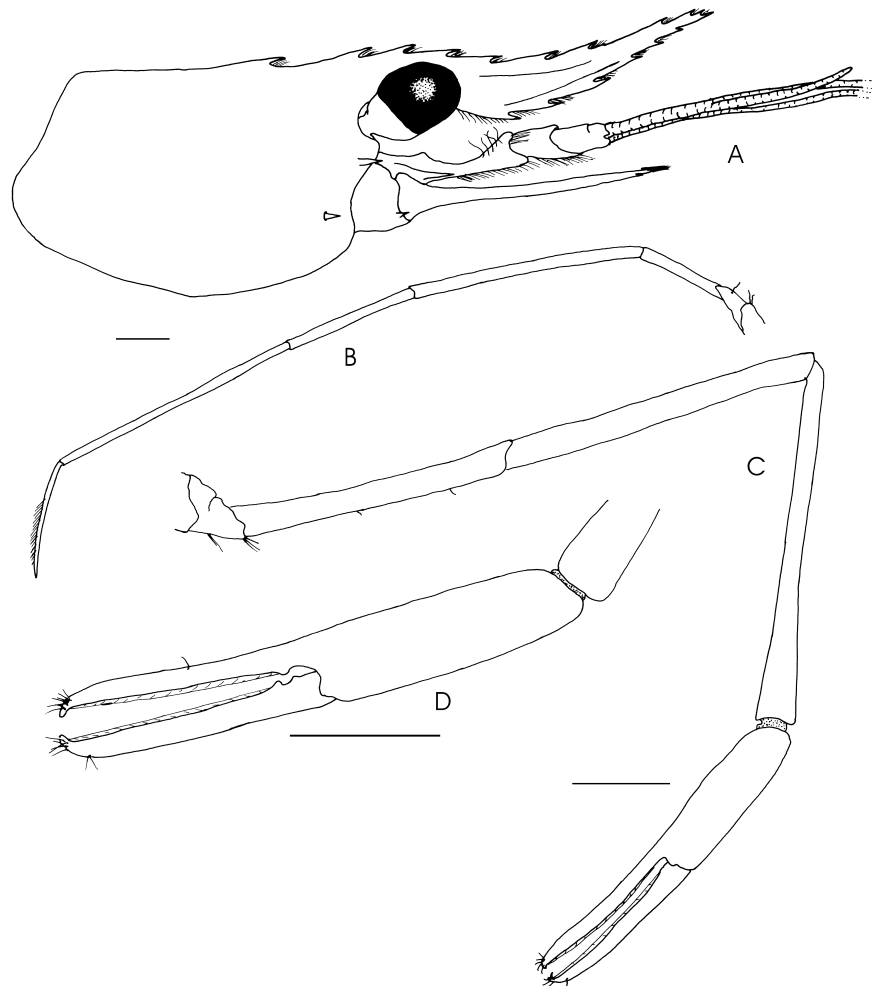
**Size.** — Maximum postorbital carapace length about 9 mm (Chace & Bruce, 1993)

**Colouration.** — Not known.

**Habitat.** — High salinity brackish waters (Johnson, 1961).

**Distribution.** — Singapore, China and now Taiwan.

**Remarks.** — The present material agrees well with the description provided by Holthuis (1952b) and the figures of Li et al (2007) and represent the first record of this poorly known species from Taiwan. In his supplementary description of *Leandrites stenopus* Holthuis, 1950, Bruce (2000) noted the presence of a small pre-terminal tooth on each of the fingers of the chela of the first pereiopod, suggesting these could have been easily overlooked in other species of the genus; however, no such teeth were noted in the present material of *L. deschampsi*.



**Figure 5.** *Leandrites deschampsi* (Nobili, 1903): Ovigerous female (pocl. 5.7 mm), Kaohsiung City; NTOU. A. carapace, right lateral view; B. left fifth pereiopod, lateral view; C. right second pereiopod, lateral view; D. same, chela, mesial view. Scale bars indicate 1.0 mm.

***Nematopalaemon* Holthuis, 1950**

*Nematopalaemon* Holthuis, 1950: 44. [type species *Leander tenuipes* Henderson, 1893, by original designation. Gender: masculine]

**Diagnosis.** — Rostrum with elevated basal crest; carapace with marginal branchiostegal spine, without branchiostegal suture or hepatic spine; stylocerite with dorsal tooth; mandible with palp; pereiopods three to five with dactyli simple, not biunguiculate, longer than propodus; first pleopod of male without appendix interna on endopod.

**Remarks.** — The genus *Nematopalaemon* is highly distinctive within the Palaemoninae. The characteristically crested rostrum, greatly elongated dactyli of the posterior two pairs of pereiopods, dorsal tooth on the stylocerite and the lack of a branchiostegal suture instantly distinguish this genus from any other.

The five species currently assigned to *Nematopalaemon* have a rather disjunct distribution through the tropics. Only the type species, *N. tenuipes*, is currently known from Asia. A key to the known species of *Nematopalaemon* is provided by Chace and Bruce (1993).

***Nematopalaemon tenuipes* Henderson, 1893**

*Leander tenuipes* Henderson, 1893: 440; plate 40, figs. 14-15. [type localities: Bombay; Gulf of Martaban; Madras]

*Palaemon luzonensis* Blanco, 1939a: 201; plate 1. [type locality: Aparri, Cagayan Province, Luzon, Philippines]

*Palaemon (Nematopalaemon) tenuipes*.—Holthuis, 1950: 44, figs. 7a-e.

*Nematopalaemon tenuipes*.—Chace & Bruce, 1993: 39.

**Material examined.** — Dongang Fishing Port, Pingtung County; 05.08.1996; 2 ♂♂, pocl. 10.5-10.6 mm; 1 ♀, pocl. 11.5 mm; 1 ovigerous ♀, pocl. 17.6 mm; NTOU.

**Diagnosis.** — Rostrum overreaching antennal scale; rostral formula: 1-3 + 5-6/2-6; shorter ramus of dorsal antennular flagellum fused for about two fifths its length; fingers of chela of second pereiopod more than twice length of carpus; 6th abdominal somite no more than 2/3 as long as postorbital carapace length.

**Size.** — Maximum total length about 70 mm (Holthuis, 1980).



**Colouration.** — Body semi-translucent with milky tinge and occasional red chromatophores; small red spots laterally on abdomen at joints of pleurae; antennae, antennules, lateral margins of telson and uropods and rostrum tinged red; eggs deep yellow.

**Habitat.** — Littoral, shallow water to about 20 m. Brackish and marine.

**Distribution.** — India, Burma, Thailand, Philippines and Taiwan. Records from South Africa, Somalia and New Zealand require confirmation. Chace and Bruce (1993) cite Taiwan in the distribution of this species but it is unclear where this record originates. The present material confirms the presence of the species in Taiwan.

**Remarks.** — Chace and Bruce (1993) suggested that a thorough review of *N. tenuipes* material from the entire Indo-pacific region was desirable to confirm the specific status of *N. colombiensis* Squires and Mora, 1971 which differs from *N. tenuipes* by the proportionally longer sixth abdominal somite ( $3/4$  as long as carapace in *N. colombiensis* vs. at most  $2/3$  as long as carapace in *N. tenuipes*). In the limited Taiwanese material available the sixth abdominal somite varies between 0.57 and 0.63 as long as the carapace.

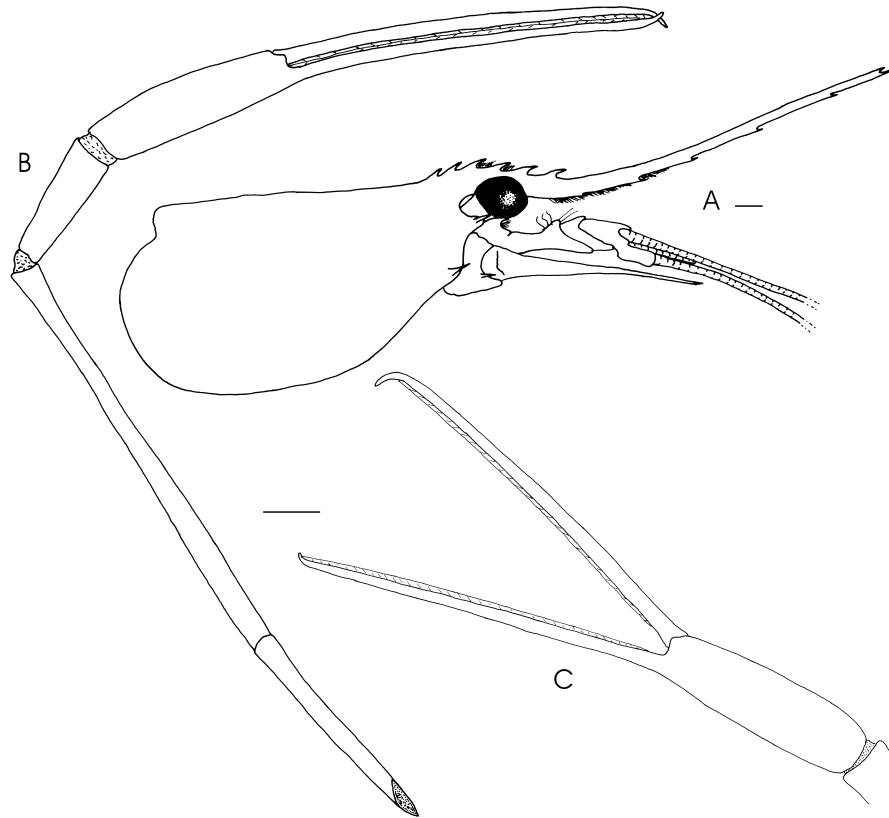


**Figure 6.** *Nematopalaemon tenuipes* Henderson, 1893: collection details and sex unknown; NTOU. Photo by T.-Y. Chan.

*Palaemon luzonensis* described by Blanco (1939a) was considered by Holthuis (1950) to be synonymous with *N. tenuipes*, however a number of discrepancies may be noted between Blanco's species and *N. tenuipes*. Blanco's figure clearly shows the fourth and fifth abdominal pleurae to be acutely produced whereas *N. tenuipes* has rounded pleurae, as figured by Kemp (1917) and mentioned as a diagnostic character of the genus by Holthuis (1952a). In addition Blanco (1939a) mentions that the telson is devoid of dorsal spines and bears only a single pair of spines on the posterior margin. Kemp (1917) noted that the telson "sometimes bears a pair of small spinules near the distal end. The apex, when perfect, is seen to bear a single pair of lateral spinules...". Contrary to this, Holthuis (1950) stated that all his material bore two pairs of dorsal spines and two pairs of posterior spines, although this observation was based on just three specimens. The ovigerous female examined here has a damaged telson but the remaining specimens bear two pairs of dorsal spines and two pairs of posterior spines. The variability of the spines on the telson, particularly those of the posterior margin which are usually considered diagnostic of the subfamily, requires more investigation.

As is common in preserved material of *Nematopalaemon*, the characteristically elongated dactyli of the third to fifth pereopods are damaged and missing in the present specimens.

*Nematopalaemon tenuipes* is a commercially important species throughout much of its range (Holthuis, 1980).



**Figure 7.** *Nematopalaemon tenuipes* Henderson, 1893: A&B, female (pocl. 11.5 mm), C, detached in pot; Dongang, Pingtung County; NTOU. A. carapace, right lateral view; B. left second pereiopod, lateral view; C. right second pereiopod, chela, mesial view. Scale bars indicate 1.0 mm.

### *Palaemon* Weber, 1795

*Palaemon* Weber, 1795: 94. [type species *Palaemon adspersus* Rathke, 1837, by direction under the plenary power of the ICZN. Gender: masculine. Name placed on the Official List of Generic Names in Zoology in Opinion 564 in 1959]

**Diagnosis.** — Rostrum without elevated basal crest; carapace with branchiostegal spine and branchiostegal suture, without hepatic spine; mandible usually with palp; third to fifth pereiopods with dactyli simple, shorter than propodus; propodus of fifth pereiopod with well developed grooming brush; endopod of first pleopod of male without marginal appendix, except in *P. concinnus*.

**Remarks.** — *Palaemon* is the second largest genus in the subfamily after *Macrobrachium*. Currently 41 species of *Palaemon* are considered valid; they are

distributed in tropical and temperate waters worldwide, reaching a maximum diversity in the Indo-Pacific. Seven species of *Palaemon* are reported from Taiwan below.

*Palaemon* is separated from the closely allied genus *Palaemonetes* Heller, 1869 by the presence of a mandible palp. A subgenus, *Palaeander*, was erected by Holthuis (1950) which is characterised by possessing a two segmented rather than three segmented mandible palp. Studies by Fujino and Miyake (1968) and Chace (1972) have demonstrated significant variation in the number of segments of the mandible palp and even its presence. The subgenus *Palaeander* is not currently recognised (Chace & Bruce, 1993) and the status of *Palaemonetes* has been questioned (Kemp, 1925; Chace, 1972).

### Key to species of *Palaemon* from Taiwan

1. Carpus of second pereiopod shorter than chela .....2
- Carpus of second pereiopod more than 1.5 times length of chela .....4
2. Rostrum with more than 5 ventral teeth; carpus of first pereiopod twice length of chela.....*Palaemon ortmanni*
- Rostrum with fewer than 5 ventral teeth; carpus of first pereiopod 1.5 times length of chela or less.....3
3. Fifth abdominal pleuron with quadrate distoventral margin; basal antennular segment with distolateral spine distinctly overreaching convex distal margin of segment; rostrum with 6-9 dorsal teeth (excluding subapical teeth) .....*Palaemon pacificus*
- Fifth abdominal pleuron with a small distoventral tooth; basal antennular segment with distolateral spine barely, if at all, overreaching convex distal margin of segment; rostrum with 7-13 dorsal teeth (excluding subapical teeth) .....*Palaemon serrifer*
4. First pleopod of male with marginal appendix on endopod; free portion of shorter ramus of dorsal antennular flagellum 3.5-6 times as long as fused part; basal antennular segment with disto-lateral spine distinctly overreaching adjacent convex distal margin of segment .....*Palaemon concinnus*

- First pleopod of male without marginal appendix on endopod; free portion of shorter ramus of dorsal antennular flagellum approximately equal in length to fused part; basal antennular segment with disto-lateral spine falling short of adjacent convex distal margin of segment.. *Palaemon debilis*

***Palaemon concinnus* Dana, 1852**

*Palaemon concinnus* Dana, 1852: 26. [type locality: Fiji]

*Palæmon exilimanus* Dana, 1852: 26. [type locality: Fiji]

*Leander longicarpus* Stimpson, 1860: 40. [type locality: Hong Kong]

*Palæmon lagdaoensis* Blanco, 1939b: 167; plate 1. [type locality: Cagayan River, Philippines]

*Palaemon (Palaemon) concinnus*.—Holthuis, 1950: 61, figs. a-h.

*Palaemon concinnus*.—Chace & Bruce, 1993: 40.—Shy & Yu, 1998: p. 45.—Jeng, 1998: p. 37, unnumbered fig.—Lin, 2007: p. 168.—Li et al., 2007: 146, figs. 58a-k.

**Material examined.** — Jialeshuei Village, Pingtung County; 26.07.2009; 3 ovigerous ♀♀, pochl. 10.3-12.5 mm; 3 ♂♂, pochl. 8.4-9.5 mm; 6 ♀♀, pochl. 10.2-12.4 mm; OUMNH-ZC 2010-02-0079.

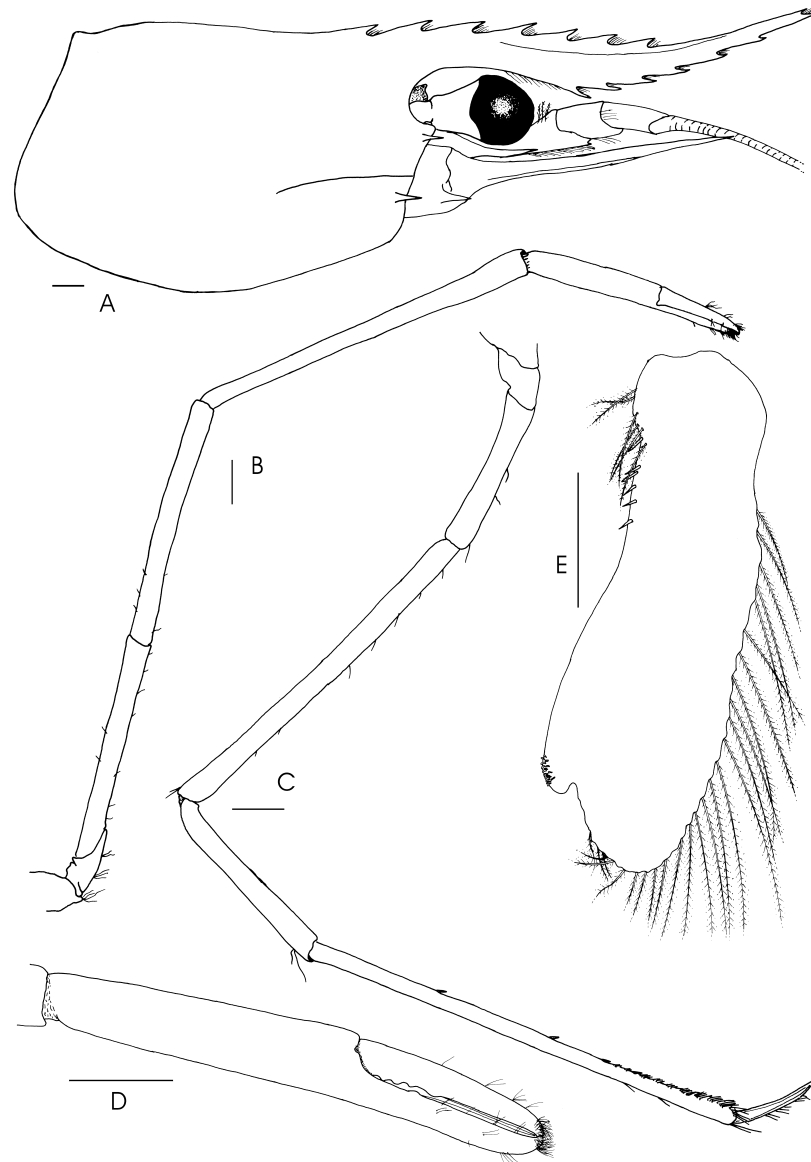
**Diagnosis.** — Rostrum slightly ascendant in distal half, tapering gradually; rostral formula 1+5-8/3-7; basal antennular segment with disto-lateral spine distinctly overreaching adjacent convex distal margin of segment; free portion of shorter ramus of dorsal antennular flagellum 3.5-6 times as long as fused part; mandible with 3 segmented palp; first pereopod with carpus 2.5-3 times as long as chela; second pereopod with carpus 1.5-2.0 times length of chela; fifth abdominal pleuron with distoventral tooth; 1st pleopod of male with marginal appendix on endopod.

**Size.** — Maximum postorbital carapace length probably about 13 mm (Chace & Bruce, 1993), maximum total length 66 mm (Holthuis, 1980).



**Figure 8.** *Palaemon concinnus* Dana, 1852: Ovigerous female (pocl. 12.5 mm); Jialeshuei Village, Pingtung County; OUMNH-ZC 2010-02-0079. Photo by T.-Y. Chan.

**Colouration.** — Rostrum largely transparent with few chromatophores distally; scattered chromatophores forming weak red-brown lines on carapace; more dense chromatophores forming a strong horizontal band across the abdominal pleurae; weak brown spot laterally on the joint between the fourth and fifth and fifth and sixth abdominal somites; a dark spot is present sub-cuticularly at the posterior end of the sixth abdominal somite; joint between the carpus and chela of second pereopod orange, slight orange colouration at joint between carpus and merus; third to fifth



**Figure 9.** *Palaemon concinnus* Dana, 1852: A-D, female (pocl. 11.7 mm; OUMNH-ZC 2010-02-0079), E, male (pocl. 9.2 mm; OUMNH-ZC 2010-02-0079); Jialeshuei Village, Pingtung County. A. carapace, right lateral view; B. right second pereiopod, lateral view; C. right fifth pereiopod, mesial view; D. right second pereiopod, chela, mesial view; E. first pleopod of male, posterior view. Scale bars indicate 1.0 mm.

pereiopods with red-orange pigment at joint between propodus and carpus and carpus and merus; eggs creamy white.

**Habitat.** — Recorded from fresh, brackish and salt waters. It is unclear if *P. concinnus* occurs in all three water types across its distribution (De Grave et al., 2008). It appears to typically inhabit fresh or slightly brackish waters and records

from strictly marine habitats, such as those of Unsworth et al. (2007), require confirmation.

**Distribution.** — Widely distributed in the Indo Pacific. Suez to South Africa and eastward to Hong Kong, Philippines, Indonesia, to Marshall Islands, French Polynesia and Fiji. Photographs of this species from Taiwan are provided by Shy and Yu (1998), Jeng (1998) and Lin (2007).

**Remarks.** — *Palaemon concinnus* differs from all other members of the genus by having a rudimentary appendix on the endopod of the first pleopod of males. Within the subfamily, this character is also found in males of *Leander*, *Leandrites*, *Brachycarpus* and *Urocaridella*.

### *Palaemon debilis* Dana, 1852

*Palaemon debilis* Dana, 1852: 26. [type locality: Hawaii]

*Leander gardineri* Borradaile, 1901: 98. [type locality: fresh-water kuli in Ekasdu, Miladummadulu Atoll, Maldives]

*Leander beauforti* Roux, 1923: 18; figs. 1-2. [type locality: Ceram Island, Kairatoe, Indonesia]

*Palaemonetes pacificus* Gurney, 1939: 145; plates 5-6. [type locality: brackish canal at Charanka in the island of Saipan, Marianne Islands]

*Palaemon (Palaemon) debilis*.—Holthuis, 1950: 66, figs. 13a-i.

*Palaemon debilis*.—Chace & Bruce, 1993: 40.—Li et al., 2007: 147, figs. 59a-d.

**Material examined.** — No Taiwanese material was available for examination.

**Diagnosis.** — Rostrum strongly ascendant distally, tapering gradually; rostral formula 1+5-8/3-10; basal antennular segment with disto-lateral spine falling short of adjacent convex distal margin of segment; free portion of shorter ramus of dorsal antennular flagellum approximately equal in length to fused part; mandible with or without palp, when present 1, 2 or 3 segmented; first pereopod with carpus more than twice times as long as chela; second pereopod with carpus more than twice as long as chela; fifth abdominal pleuron acute distoventrally; 1st pleopod of male without marginal appendix on endopod.

**Size.** — maximum postorbital carapace length probably no more than 10 mm (Chace & Bruce, 1993).



**Colouration.** — Rostrum largely transparent, ventral margin dark red from about mid length to tip, dorsal margin with yellow or white chromatophores with further, larger chromatophores occurring in proximal half of the rostrum; scattered chromatophores forming weak red-brown lines on carapace, a horizontal line occurs in the gastric region of the carapace and another line approximately follows the branchiostegal groove; the abdomen is covered with further scattered chromatophores, the joints between the abdominal segments are tinged orange dorsally; a weak orange spot occurs at the joints between the fourth and fifth and fifth and sixth abdominal somites; a pronounced dark fleck occurs dorsolaterally at the posterior margin of the third abdominal somite and a further dark spot is found laterally at the posterior margin of the sixth abdominal somite; the bases of the pleopods are tinged yellow-orange; the telson and the uropods are faintly tinged orange; the pereopods are mostly transparent but may have some whitish markings at the propodus/merus joint; the scaphocerite has orange margins; a large orange spot occurs distally on the basal segment of the antenna; the antennulae are banded with white pigment; egg colour unknown.

**Habitat.** — Fresh, brackish and salt waters. It is unclear if *P. debilis* occurs in all three water types across its distribution (De Grave et al., 2008).

**Distribution.** — Red Sea to South Africa to Ryukyu Islands, Philippines and Indonesia, Great Barrier Reef of Australia, and eastward to Hawaii and the Tuamotu Archipelago. *Palaemon debilis* was reported from Taiwan by Maki and Tsuchiya (1923) with this record later being cited by Holthuis (1950). The photo in Maki and Tsuchiya (1923) bears a superficial resemblance to *P. debilis* but is rather unclear and may conceivably refer to a different species. As no material of this species is available from Taiwan its occurrence cannot be verified. However, as this species has a very broad reported distribution range, which would include Taiwan, it could be expected to occur.

**Remarks.** — A redescription of *P. debilis* based on Hawaiian material (Chace, 1972) revealed that the mandible palp shows variation in the number of segments with a tendency to be absent. Fujino and Miyake (1968) showed similar variation in the number of segments of the mandible palp of *P. debilis* although none of their 22 specimens lacked the palp. De Grave and Al-Maslamani (2006) suggested that *P. debilis* may represent a species complex.

Surprisingly, despite being widely recorded in the literature, the colour pattern of *P. debilis* has not been previously described. The pattern given above is based on

colour photographs of the species from French Polynesia given by Keith et al. (2002) and Keith and Vigneux (2002).

***Palaemon ortmanni* Rathbun, 1902**

*Palæmon ortmanni* Rathbun, 1902: 53. [replacement name for *Leander longipes* Ortmann, 1890 not De Haan, 1849]

*Leander longipes* Ortmann, 1890: 519; plate 37, fig. 13. [type locality: Sagami Bay, Japan]

*Palaemon (Palaemon) ortmanni*.—Holthuis, 1950: 80, figs. 17a-g.—Chan & Yu, 1985: 120, text figs. 2a-f.

*Palaemon ortmanni*.—Li et al., 2007: 154, fig. 63.

**Material examined.** — Bachimen Port, Keelung City; 12.05.1984; 1 ♂, pocl. 8.8 mm; 6 ♀♀, pocl. 16.7-17.6 mm; NTOU. Bachimen Port, Keelung City; 14.08.1988; 1 ♀, pocl. 10.4 mm; NTOU. Taiwan; 1 ♀, pocl. 5.2 mm; NTOU.

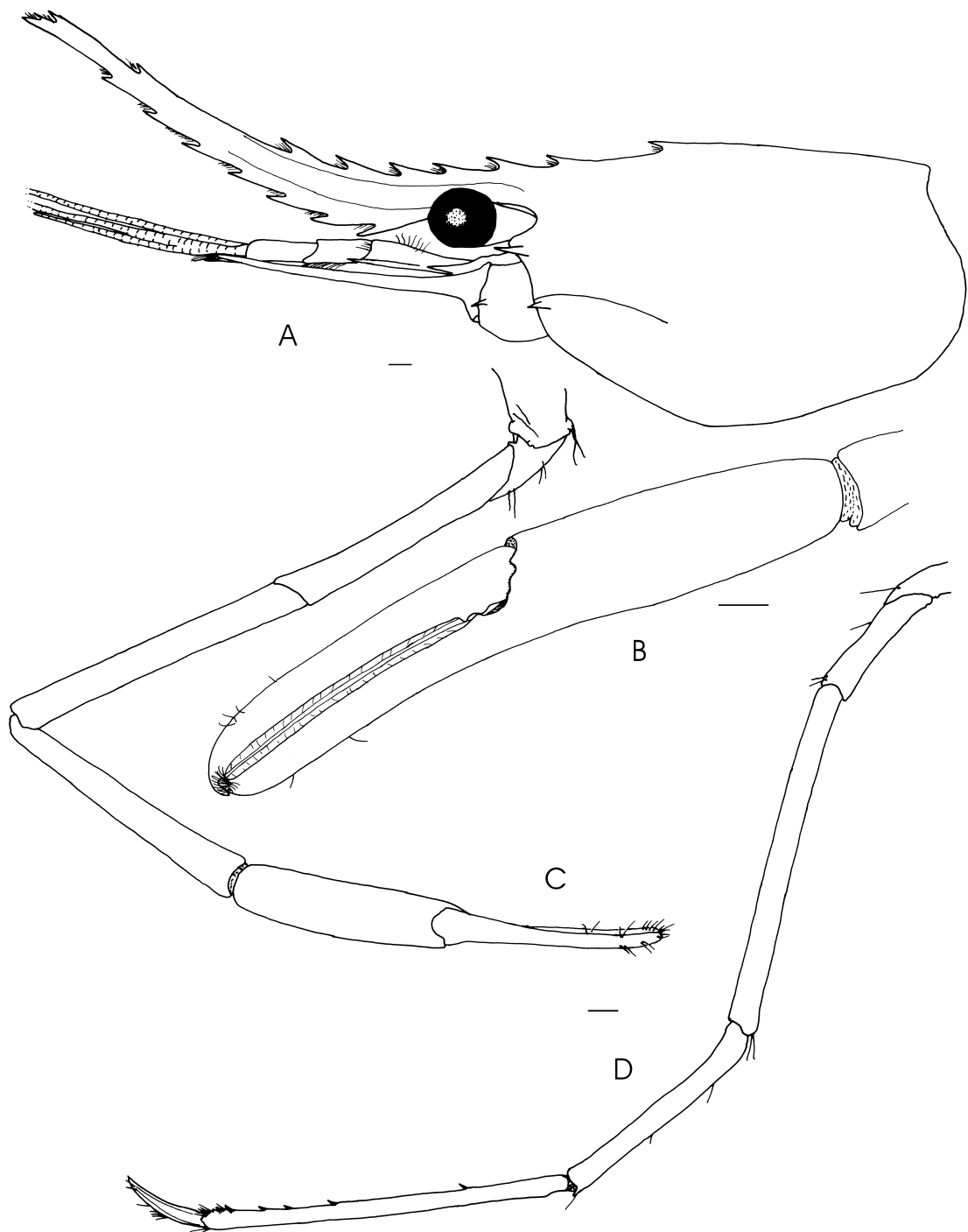
**Diagnosis.** — Rostrum strongly ascendant in anterior half, tapering gradually; rostral formula 1-3+7-9/5-9; basal antennular segment with disto-lateral spine distinctly overreaching adjacent convex distal margin of segment; free portion of shorter ramus of dorsal antennular flagellum 2.3-3.5 times as long as fused part; mandible with 3 segmented palp; first pereiopod with carpus twice as long as chela; second pereiopod with chela 1.5-1.8 times length of carpus; fifth abdominal pleuron with distoventral tooth; 1st pleopod of male without marginal appendix on endopod.

**Size.** — Maximum total length 78.5 mm (Holthuis, 1980)

**Colouration.** — Cephalothorax with strong horizontal and diagonal red pigment lines; first to fourth abdominal pleurae with strong vertical pigment bands, fifth and sixth with strong horizontal pigment bands; distal end of uropods tinged orange; third to fifth pereiopods with orange pigment at joints between segments; fingers of chela of second pereiopod with red, yellow and orange bands, palm with purple band, distal end of carpus with purple and yellow band, distal end of other segments with purple and orange bands; egg colour unknown.

**Habitat.** — Rocky shores, over sand or muddy bottoms, under or around rocks.

**Distribution.** — Japan and China. Previously recorded from Taiwan by Chan and Yu (1985).



**Figure 11.** *Palaemon ortmanni* Rathbun, 1902: Female (pocl. 17.6 mm); Bachimen Port, Keelung City; NTOU. A. carapace, left lateral view; B. left second pereiopod, chela, mesial view; C. left second pereiopod, lateral view; D. right fifth pereiopod, lateral view. Scale bars indicate 1.0 mm.

**Remarks.** — Holthuis (1950) suggested that, given examination of more material, *P. ortmanni* and *P. gravieri* may prove to represent two extremes of variation of a single species. In fact, a number of important differences may be found between the two species. The rostra are clearly different shapes being nearly straight in *P. gravieri* and greatly upturned in *P. ortmanni*, there are fewer teeth on the upper margin of the rostrum in *P. ortmanni* than *P. gravieri*, the datyli of the ambulatory pereopods are more slender and curved in *P. gravieri* than *P. ortmanni*, *P. ortmanni* has a much stronger colour pattern in life than *P. gravieri*.

The study on the mandible palp conducted by Fujino and Miyake (1968) found no variation in the number of mandible palp segments of *P. ortmanni*. In the present material a female (pocl. 17.6 mm) has a one segmented palp on the left mandible whilst that of the right mandible is normal. However, there is evidence of damage to this structure and it is likely that this is the cause in this case rather than a natural mutation.

### *Palaemon pacificus* (Stimpson, 1860)

*Leander pacificus* Stimpson, 1860: 40. [ad insulas “Hong Kong” et “Hawaii” etiam in portu “Simoda”]

?*Leander okiensis* Kamita, 1950: 216; fig. 2. [innermost coast of Suwa Bay]

*Palaemon (Palaemon) pacificus*.—Holthuis, 1950: 87, figs. 19a-g.—Chan & Yu, 1985: 122, text figs. 3a-f.

*Palaemon pacificus*.—Chace & Bruce, 1993: 41.—Li et al., 2007: 155, figs. 60a-g.

?*Palaemon serrifer*.—Jeng, 1998: p. 37, unnumbered fig.

**Material examined.** — Keelung Ho-Ping Island Park; 26.06.2008; 1 ♂, pocl. 7.5 mm; OUMNHZC 2008-18-0024. Badouzih, Keelung City; 04.06.1984; 3 ♂♂, pocl. 4.9-7.8 mm; 5 ♀♀, pocl. 5.6-15.8 mm; 4 ovigerous ♀♀, pocl. 14.5-15.2 mm; NTOU. Taiwan; 2 ♂♂, pocl. 5.6, 6.0 mm; 3 ♀♀, pocl. 4.3-6.5 mm; NTOU.

**Diagnosis.** — Rostrum ascendant in distal half, tapering gradually; rostral formula 1-3+6-9/3-5; basal antennular segment with disto-lateral spine distinctly overreaching adjacent convex distal margin of segment; free portion of shorter ramus of dorsal antennular flagellum 3-4 times as long as fused part; mandible with 3 segmented palp; first pereopod with carpus 1.6 times as long as chela; second pereopod with chela

1.3-1.4 times length of carpus; fifth abdominal pleuron quadrate distoventrally; 1st pleopod of male without marginal appendix on endopod.

**Size.** — Maximum postorbital carapace length probably little more than 10 mm (Chace & Bruce, 1993), 15.8 mm (present material), maximum total length 53 mm (Holthuis, 1980).

**Colouration.** — Pattern similar to that of *P. ortmanni* but deeper and more defined. Cephalothorax with strong horizontal and diagonal red-brown pigment lines; first to fourth abdominal pleurae with strong vertical red-brown pigment bands, diffuse orange pigment bands accompany the red-brown bands and a further orange spot may be found laterally; sixth pleuron with strong horizontal pigment band and orange spot distally; distal end of uropods tinged orange and dark red-brown; pereopods with purple and orange bands at joints between segments; eggs olive-green.

**Habitat.** — Marine, occasionally brackish water.

**Distribution.** — Widespread in the Indo-Pacific from the Suez Canal and Red Sea and eastern Africa, India, Hong Kong, Japan, Indonesia, New Caledonia, and Hawaii. Its occurrence in South Africa requires confirmation since MacPherson (1990) validated *Palaemon peringueyi* (Stebbing, 1915) for the South African form.

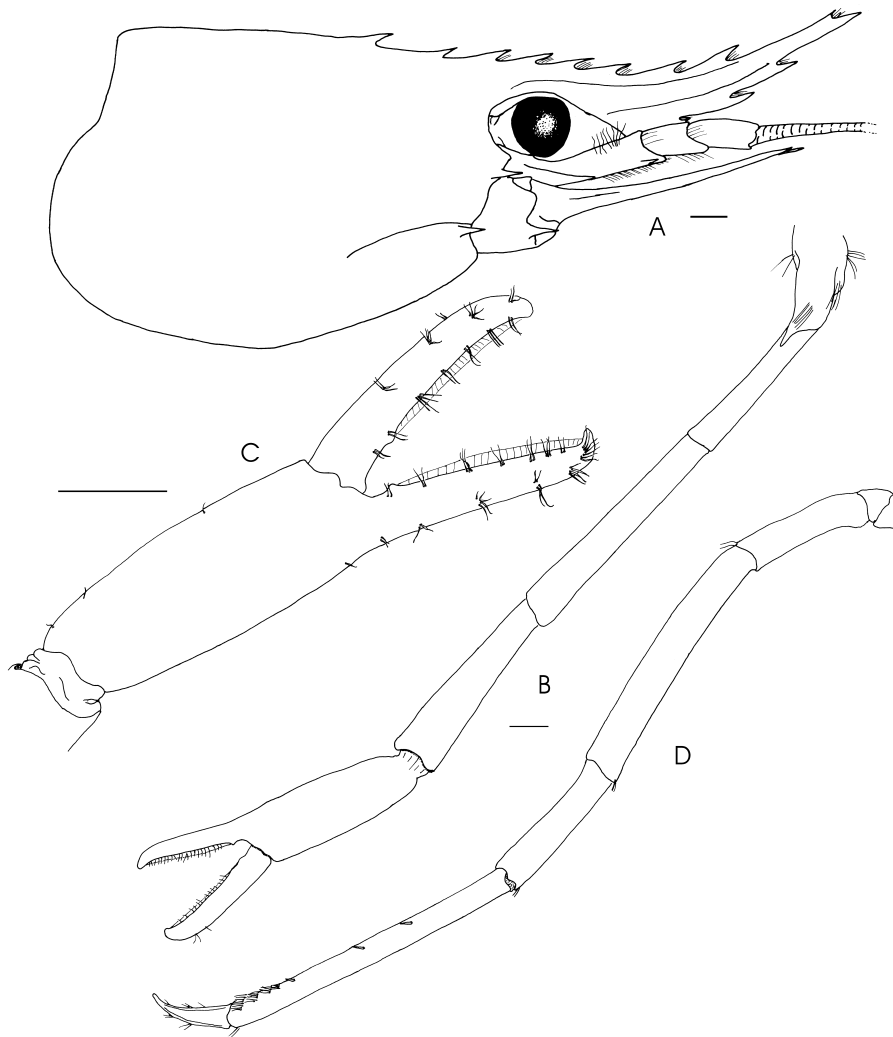
*Palaemon pacificus* has previously been reported from Taiwan by Chan and Yu (1985) from Keelung City and Taipei County. A photograph recorded as *P. serrifer* from Kenting (Jeng, 1998) is also tentatively referred to this species. The colour pattern of the specimen in this photograph does not match either species but there is a tendency in *Palaemon* to lose distinct colour patterns in low light conditions or turbid waters. Based on the observable morphological characters, particularly the rostrum, it appears to be *P. pacificus*.

**Remarks.** — The material examined here agrees well with previous descriptions of the species (Holthuis, 1950; MacPherson, 1990; Nguyễn, 1992; Li et al., 2007). The species normally has a three segmented mandible palp but a small number of specimens possessing a two segmented mandible palp on one or both sides were reported by Fujino and Miyake (1968). All the Taiwanese specimens examined here had a three segmented palp on both mandibles.

Holthuis (1980) included *Leander okiensis* Kamita, 1950 as a junior synonym of *P. pacificus*. This species is undoubtedly based on a specimen with a malformed rostrum and Holthuis (1980) is most likely correct in his assumption that it is *P.*

*pacificus*, a fact supported by its co-occurrence with that species, although Kamita (1950) states that the colour in life resembles that of *P. serrifer*.

Colour photographs provided by Chang and Chen (1992, p. 104), Tzeng and Chan (1992, p. 88) and Hung (2000, p 113) appear to be of *Palaemon pacificus* whilst that of Jeng, (1998, p. 37) labelled *P. serrifer* is tentatively referred to *P. pacificus*.



**Figure 13.** *Palaemon pacificus* (Stimpson, 1860): Female (pocl. 15.6 mm); Badouzih, Keelung City; NTOU. A. carapace, right lateral view; B. right second pereiopod, mesial view; C. same, chela, mesial view; D. right fifth pereiopod, lateral view. Scale bars indicate 1.0 mm.

*Palaemon serrifer* (Stimpson, 1860)

*Leander serrifer* Stimpson, 1860: 41. [type locality: Portu “Hong Kong” et sinibus insulae “Ousima”, littoralis]

*Leander Fagei* Yu, 1930: 555, 561; fig. 2. [type locality: Pèninsule de Shantong]

*Leander serrifer* var. *longidactylus* Yu, 1930: 570 (partim); text figs. (not fig. 4b'-c'). [Yangmataoa, Peitaiho, Tangkou, Chefoo]

*Palaemon (Palaemon) serrifer*.—Holthuis, 1950: 83, figs. 18a-g.—Chan & Yu, 1985: 123, text figs. 4a-e.

*Palaemon serrifer*.—Chace & Bruce, 1993: 41.—Li et al., 2007: 159, figs. 66a-d.—Dai et al., 2009: 60.—Hung, 2000: 114, fig. 342.

*Palaemon (Palaemon) macrodactylus*.—Chan & Yu, 1985: 119, text figs. 1a-e (not *Palaemon macrodactylus* Rathbun, 1902).

?Not *Palaemon serrifer*.—Jeng, 1998: 37, unnumbered fig.

**Material examined.** — Shalun, Taipei County; beach; hand net; 18.06.1990; leg. P.H. Ho; 1 ♂, pocl. 5.3 mm (with bopyrid parasite); 2 ♀♀, pocl. 5.6-6.9 mm; NTOU. Zhuwei, Taipei County; 17.06.1990; 3 ♂♂, pocl. 4.3-5.2 mm; 4 ♀♀, pocl. 4.5-6.8 mm; NTOU. Badouzi, Keelung City; 28.05.1984; 1 ovigerous ♀, pocl. 12.5 mm; NTOU. Badouzi, Keelung City; 04.06.1984; 1 ♂, pocl. 7.1 mm; NTOU. Taiwan; 9 ♂♂, pocl. 4.8-9.4 mm; 11 ♀♀, pocl. 4.6-7.8 mm; NTOU. Bachimen, Keelung City; rocky shore; hand net; 1995; 2 ovigerous ♀♀, pocl. 10.2, 10.3 mm; NTOU. Donggang, Pingtung County; aquaculture pond; 07.06.1984; leg. T.-Y. Chan; 9 ♂♂, pocl. 5.0-6.0 mm; NTOU. Penghu County; 09.07.1997; 1 ♀, pocl. 5.5 mm; 1 ovigerous ♀, pocl. 6.3 mm; NTOU. Cingluo, Penghu County; 25.04.1992; 1 ♀, pocl. 8.9 mm; NTOU. Guanyinting, Penghu County; 20.04.2002; 2 ♂♂, pocl. 5.2, 6.4 mm; 1 ♀, pocl. 5.7 mm; NTOU. Kaohsiung Port, Kaohsiung City; 15.04.1996; 2 ♂♂, pocl. 5.0, 6.2 mm; 1 ♀, pocl. 5.0 mm; NTOU. Donggang, Pingtung County; Aquaculture ponds; 28/07/2009; 52 ♂♂, pocl. 3.2-6.0 mm; 41 ♀♀, pocl. 4.4-8.0 mm; 24 ovigerous ♀♀, pocl. 5.2-8.1 mm; 2 post ovigerous ♀♀, pocl. 6.0, 10.0 mm; OUMNH-ZC 2010-02-0077.

**Diagnosis.** — Rostrum nearly horizontal, broad, tapering strongly or slightly ascendant distally, slender, tapering gradually; rostral formula 1-3+7-13/3-5; basal antennular segment with disto-lateral spine not overreaching adjacent convex distal margin of segment; free portion of shorter ramus of dorsal antennular flagellum 3

times as long as fused part; mandible with 3 segmented palp; first pereopod with carpus 1.4 times as long as chela; second pereopod with chela 1.3-1.4 times as long as carpus; fifth abdominal pleuron with distoventral tooth; 1st pleopod of male without marginal appendix on endopod.

**Size.** — Maximum postorbital carapace length probably about 10 mm (Chace & Bruce, 1993). Maximum total length 36 mm (Holthuis, 1980).

**Colouration.** — Carapace with two strong diagonal red-brown lines, some less defined diagonal and horizontal lines sometimes also present; scattered occasional white spots across carapace and abdomen; rostrum largely colourless but occasionally with scattered chromatophores; distal parts of the scaphocerites and antennular peduncles tinged red; joints between the first three abdominal somites with strong red-brown bands between, horizontal bands present at the base of the pleurae and on the bases of the pleopods; a small orange-yellow spot placed laterally at joint between each abdominal somite, further orange yellow spots present on the uropods; strong yellow bands around the joints of the segments of all pereopods, segments, particularly the chelae of the second pereopods with blue tinge. The long-rostrum form (see remarks below) from has a generally similar colour pattern but many of the colour bands are less well defined.



**Figure 14.** *Palaemon serrifer* (Stimpson, 1860): Ovigerous female; Donggang, Pingtung County; (OUMNH-ZC 2010-02-0077). Photo by T.-Y. Chan.

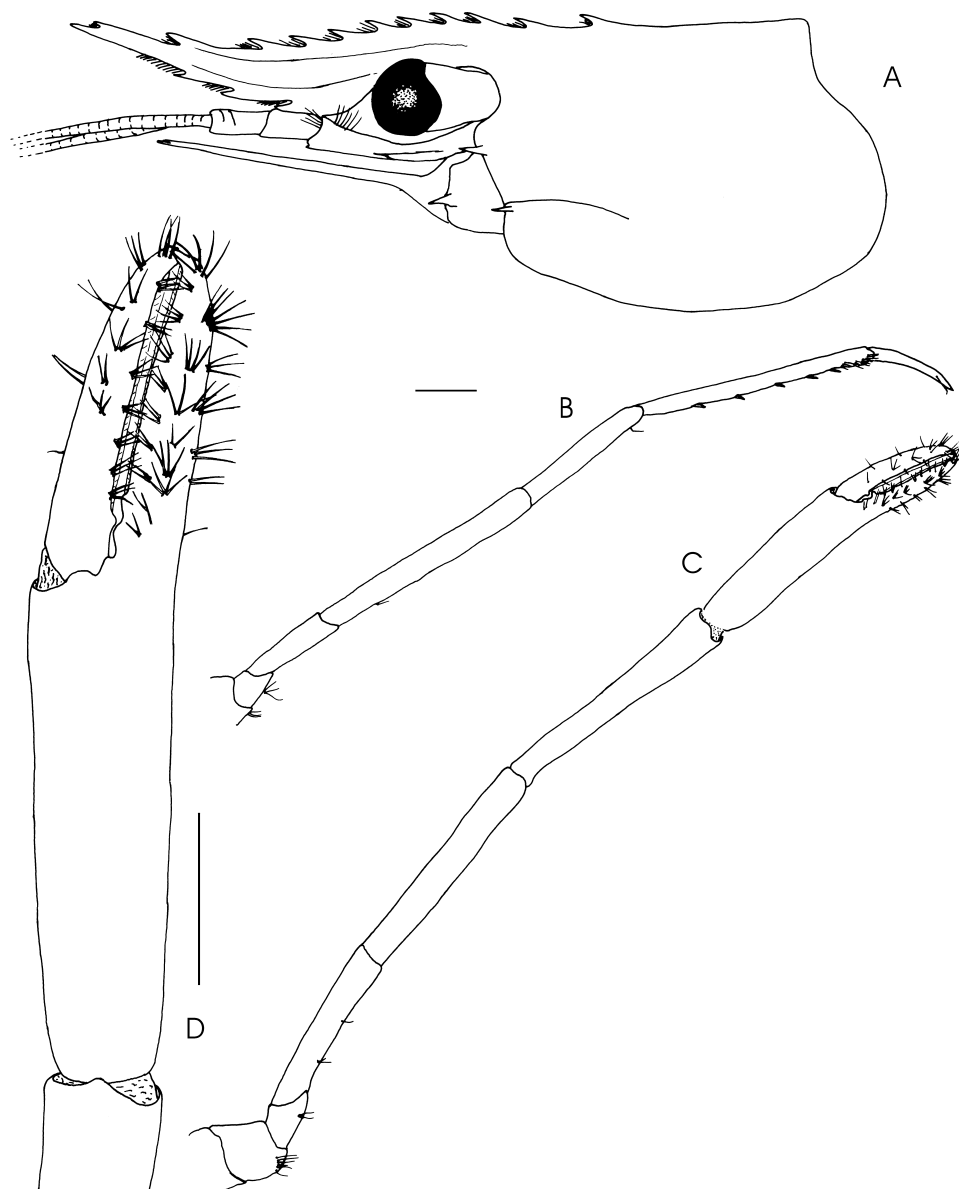


**Habitat.** — Littoral marine waters often among rocks, sometimes in high salinity parts of estuaries.

**Distribution.** — From Vladivostok and Japan southwards to Vietnam, Indonesia and northern Australia, extending westwards as far as India. *Palaemon serrifer* was previously recorded from Taiwan by Chan and Yu (1985) based on nine specimens from Pa-Tou-Tsu, Keelung City and a colour photograph in Jeng (1998). However, the photograph provided by Jeng shows a specimen with a very upturned rostrum and probably does not relate to this species. It is tentatively referred to *P. pacificus* (see remarks under that species).

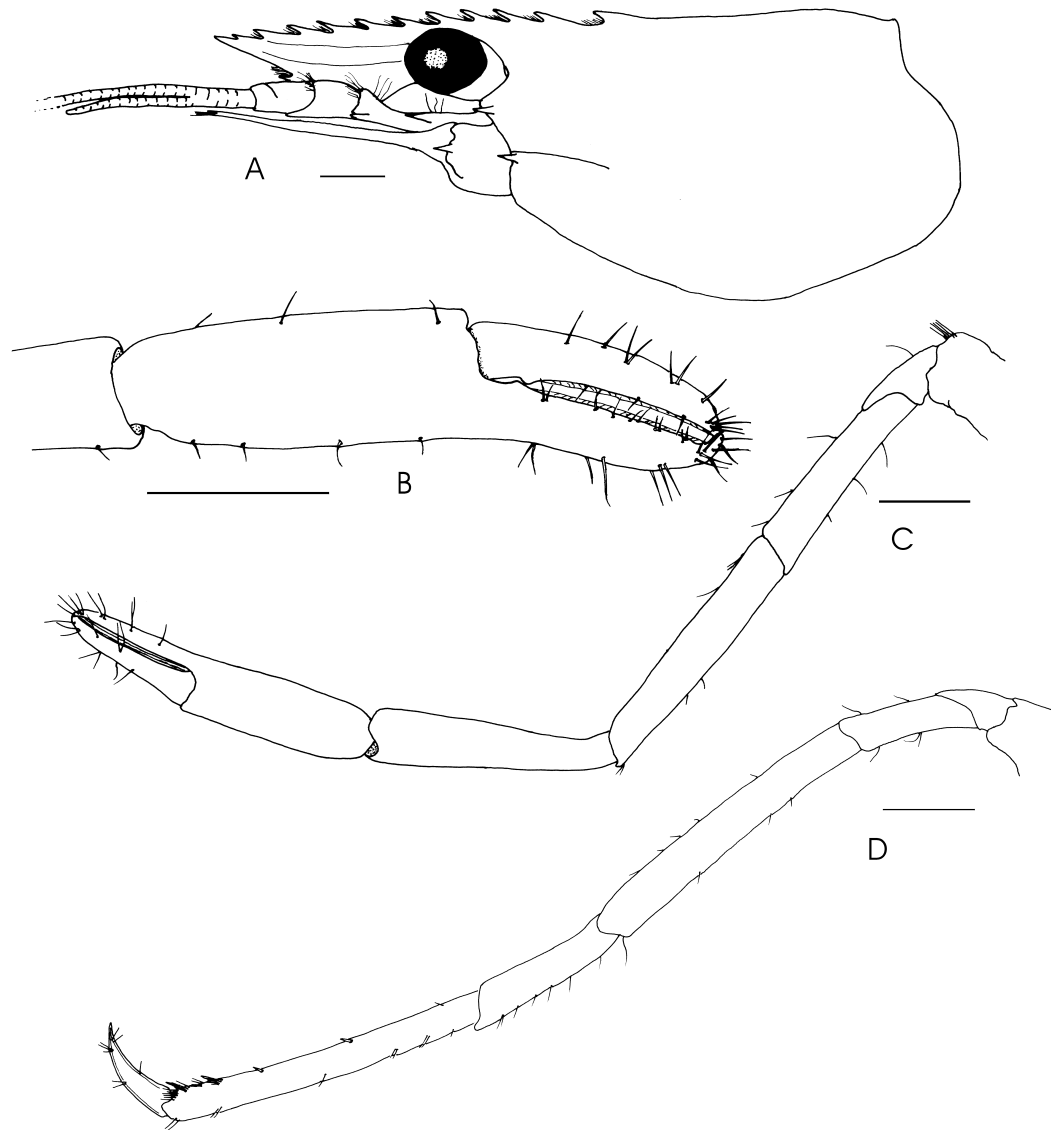
**Remarks.** — Two very distinctive forms of *Palaemon serrifer* occur in Taiwan, both of which are illustrated here. The first has a broad, straight rostrum with the dorsal teeth evenly distributed along its length, with the exception of the proximal most tooth which is slightly removed. In this form the rostrum does not overreach the scaphocerites and is shorter than the post-orbital carapace length (usually about 0.8-0.9 x  $pocl.$ ). The second form has a more slender, slightly upturned rostrum with an unarmed portion sub-distally (excluding the sub-apical teeth). In this form, the rostrum overreaches the scaphocerites by about a fifth of its length and is distinctly longer than the post-orbital carapace length (usually  $>1.1$  x  $pocl.$ ). In this respect it agrees with the description and figures. of *Leander fagei* Yu, 1930, a species currently considered synonymous with *P. serrifer*. This latter form is that reported from Taiwan by Chan and Yu (1985) as *Palaemon macrodactylus* Rathbun, 1902; it is common in a number of habitats but most of the specimens examined here originated from aquaculture ponds where it is considered a pest species (Chan & Yu, 1985). The rostra of *Palaemon* are notoriously variable (De Grave, 1999) and, although all specimens examined here were clearly assignable to one form or the other with no intermediate rostral forms being recorded, no other morphological differences between the forms were found and the two rostral forms fall within the range of variation reported for *P. serrifer* by other authors (Holthuis, 1950; Nguyễn, 1992). It is possible that examination of a larger amount of material from across the geographic range of *P. serrifer*, possibly including morphometric or genetic means, would identify other differences between the two forms but, for now, they are treated as extremes of variation of a single species.

Of the two lots reported as *P. macrodactylus* by Chan and Yu (1985), one was not available for examination here (Pa-Tou-Tsu, Keelung City, 3 June 1984); however



**Figure 15.** *Palaemon serrifer* (Stimpson, 1860): Female (pocl. 6.1 mm); Donggang, Pingtung County; OUMNH-ZC 2010-02-0077. A. carapace, left lateral view; B. right fifth pereiopod, lateral view; C. right second pereiopod, lateral view; D. same, chela, mesial view. Scale bars indicate 1.0 mm.

re-examination of some of the specimens from the second lot (Donggang, Pingtung County; 7 June 1984) shows them to belong to the longer rostrum form of *P. serrifer*. It is assumed that the same characters were used to identify the specimens in the missing lot and therefore these specimens, too, will likely be referable to *P. serrifer*. *Palaemon macrodactylus* naturally occurs in Japan, Korea and Northern China, but



**Figure 15.** *Palaemon serrifer* (Stimpson, 1860): Female (pocl. 6.5 mm); Zhuwei, Taipei County; NTOU. A. carapace, left lateral view; B. right second pereiopod, chela, mesial view; C. right second pereiopod, lateral view; D. right fifth pereiopod, lateral view. Scale bars indicate 1.0 mm.

has been introduced to a number of other temperate locations worldwide such as Western North America (Newman, 1963), Eastern North America (Warkentine & Rachlin, 2010), Argentina (Spivak et al., 2006), Australia (Holthuis, 1980; Pollard & Hutchings, 1990; Bruce & Coombes, 1997; Walker & Poore, 2003) and European coasts (Ashelby et al., 2004; Cuesta et al., 2004; d'Udekem d'Acoz et al., 2005

Beguer et al., 2007; González-Ortegón et al., 2007; Chícharo et al., 2009; Micu & Niță, 2009; Raykov, 2010). For the time being it can be removed from the list of *Palaemon* known from Taiwan.

A photograph of two shrimps in Chang and Chen (1992, p. 105) most likely refer to this species.

### ***Urocaridella* Borradaile, 1915**

*Urocaridella* Borradaile, 1915: 207. [type species *Urocaridella gracilis* Borradaile, 1915 (invalid senior synonym of *Urocaridella urocaridella* (Holthuis, 1950)), by monotypy. Gender: feminine]

**Diagnosis.** — Rostrum armed with 2 strong basal teeth; carapace with strong epigastric tooth at about mid-length of dorsal surface, with submarginal branchiostegal spine, without hepatic spine or branchiostegal suture; mandible with or without palp; third to fifth pereopods with dactyli simple, not biunguiculate, shorter than propodus; propodus of fifth pereopod without grooming brush; endopod of male first pleopod with marginal appendix.

**Remarks.** — As pointed out by Li et al. (2004), this somewhat enigmatic genus occupies an interesting position within the Palaemonidae, sharing characters from the two subfamilies, which has created complications with its systematic placement in the past. It was included in the Pontoniinae by Borradaile (1917) and Kemp (1922), whilst Holthuis (1950, 1952c) treated the genus as a synonym of *Leander*, thus transferring it to the Palaemoninae. Chace and Bruce (1993) regarded the unique form of the rostrum as being sufficient to grant generic status but retained the genus in the Palaemoninae.

*Urocaridella* species are ecologically important in coral reef environments acting as cleaner shrimps, removing parasites from fish (Becker & Grutter, 2004). Currently four species of the genus are considered valid although colour photos in Debelius (2001), Kato and Okuno (2001), Kawamoto and Okuno (2003) and Minemizu (2000) indicate a number of undescribed species may be present in the Indo-Pacific region. Two species are here reported from Taiwan.

**Key to species *Urocaridella* from Taiwan**

1. Mandible with two segmented palp; chelae of second pereopod without dentition proximally between fingers ..... *Urocaridella urocaridella*
- Mandible without palp; chelae of second pereopod with dentition proximally between fingers..... *Urocaridella antonbruunii*

***Urocaridella antonbruunii* (Bruce, 1967)**

*Periclimenes antonbruunii* Bruce, 1967: 45; figs. 19-22. [type locality: Pamanzi Island reef, Dzaoudzi, Ile Mayotte, Archipel des Comores]

*Leandrites cyrtorhynchus* Fujino & Miyake, 1969: 143; figs. 1-3. [type locality: Tôshima Island, Tanabe Bay, Wakayama Prefecture]

*Leandrites longipes* Liu, Liang & Yan, 1990b: 127; fig. 24. [type locality: Sanya, Hainan Isl., China]

*Leandrites cyrtorhynchus*.—Jeng, 1998: 118, unnumbered fig.

?Not *Urocaridella antonbruunii*.—Jeng, 1998: 119, unnumbered fig. [see Remarks below].

**Material examined.** — Hepingdao, Keelung City; 29.06.2006; 2 ovigerous ♀♀, pcl. 6.7, 8.5 mm; NTOU. Hepingdao, Keelung City; 19.05.2006; 1 ovigerous ♀, pcl. 7.3 mm; NTOU.

**Diagnosis.** — Rostrum with 1-2+2+2/6-9 teeth, excluding the epigastric tooth on the carapace; carapace with branchiostegal spine removed from margin by at least twice length of spine; mandible without palp; first pereopod with fingers subequal to palm length, chela much shorter than carpus; second pereopod with fingers more or less subequal to palm length, palm slightly shorter than carpus; third pereopod with propodus at least 4 times as long as dactyl; third abdominal somite with nearly subrectangular dorsal profile, 5th abdominal pleuron rounded posteroventrally; inner pair of posterior marginal spines on telson robust, plumose.

**Size.** — maximum post-orbital carapace length about 8.5 mm (present material).

**Colouration.** — Mainly transparent with small red dots scattered over the carapace and the first to fifth abdominal segments and a red bar across the hump of the third abdominal segment, parallel to its anterior margin. Extensive tracts of red extend

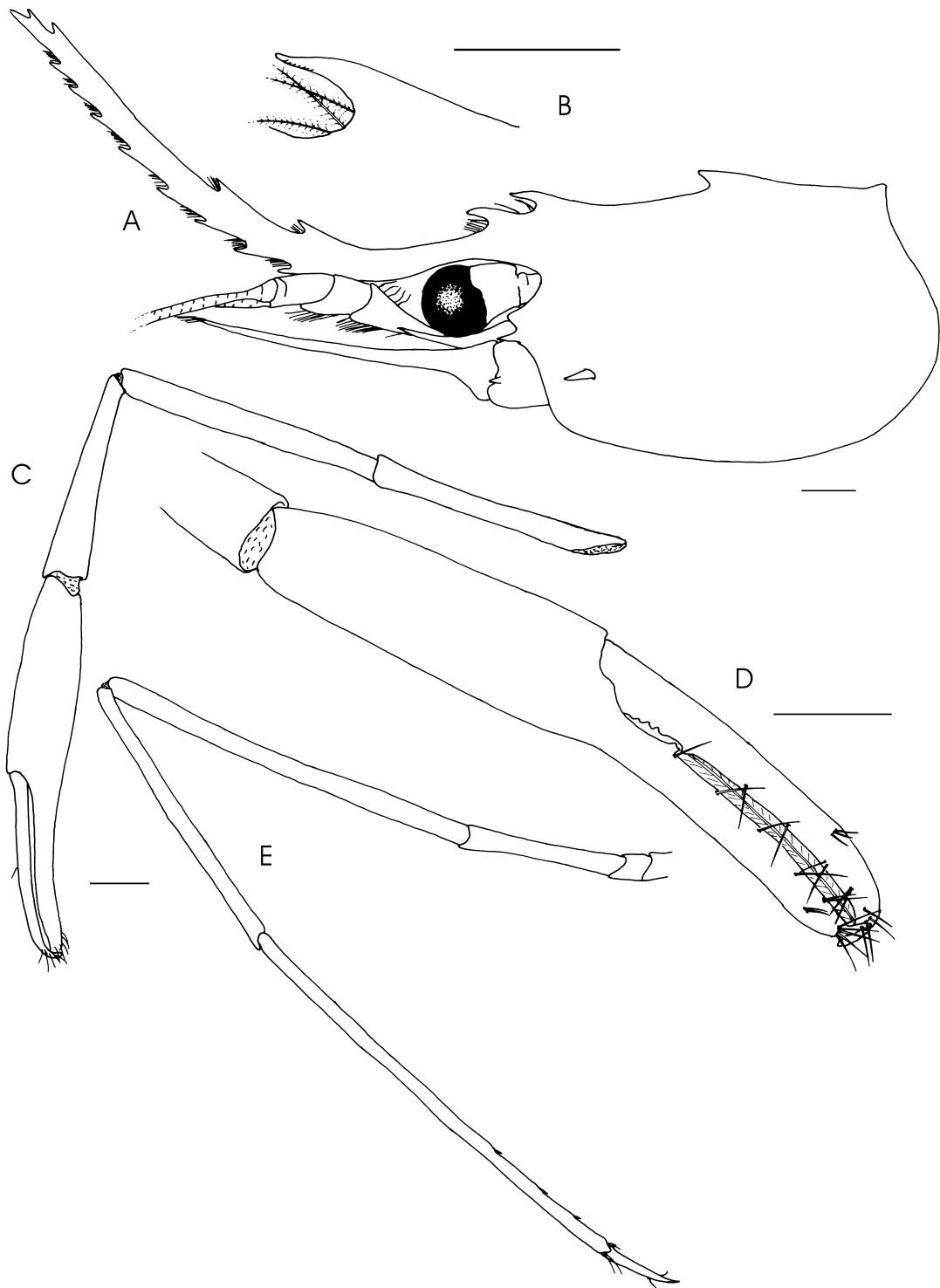
along the mid-ventral line of the abdomen with red patches also at the bases of the pleopods. Red patches are also present at the bases of third and fourth pereopods but the carpus and chela of the second pereopod are covered with scattered white dots and only a few red spots are present on the palm. Numerous red dots are present on the eyestalks, and the antennular peduncles are also red. Red subterminal spots are present on exopod and endopod of the uropods (Bruce, 1967).

**Habitat.** — Marine to a depth of about 60 m (Li & Bruce, 2006).

**Distribution.** — Comoro Islands, Japan, Indonesia, Great Barrier Reef, Palau Islands, South China Sea (Li et al., 2004). Previously reported from Taiwan by Jeng (1998 — see below).

**Remarks.** — The original description of *Periclimenes antonbruunii* given by Bruce (1967) was founded on a single specimen from the Comoro Islands. One of the unique features of the species was the presence of a small accessory spine on the dactyli of the ambulatory pereopods, making them biunguiculate. Bruce and Coombes (1995) considered that the holotype of this species was a juvenile, most likely a first post-larval stage, due to the presence of rudimentary exopods on the first and second pereopods. The very similar *U. cyrtorhynchus* (Fujino & Miyake, 1969) primarily differs in having a simple dactylus on the ambulatory pereopods. As no further specimens of *U. antonbruunii* had been recorded since the original description, whilst there had been many records of *U. cyrtorhynchus*, Bruce and Coombes (1995) regarded the two species as synonymous; they concluded that the accessory spine was probably a juvenile feature, as found some *Macrobrachium* species (see Holthuis, 1950), which is lost with maturity.

A colour photo of *U. antonbruunii* (as *Leandrites cyrtorhynchus*) from Taiwan was provided by Jeng (1998, p. 118). Conversely, *Urocaridella antonbruunii* sensu Jeng (1998, p. 119) agrees with a form reported as *Urocaridella* sp. B by Debelius (1999), Kato and Okuno (2001) and Kawamoto and Okuno (2003), and as *Urocaridella* sp. 2 by Minemizu (2000) on account of the colour pattern and highly carinate third abdominal somite. The exact identity of this form is currently under study (Okuno pers. comm.).



**Figure 16.** *Urocaridella antonbruunii* (Bruce, 1967): A, B, E, ovigerous female (pocl. 8.5 mm); C, D, ovigerous female (pocl. 6.7 mm); Hepingdao, Keelung City; NTOU. A. carapace, left lateral view; B. second basal tooth, left lateral view; C. left second pereiopod, lateral view; D. same, chela, mesial view; E. left fifth pereiopod, lateral view. Scale bars indicate 1.0 mm.

*Urocaridella urocaridella* (Holthuis, 1950)

*Leander urocaridella* Holthuis, 1950: 28. [replacement name for *Urocaridella gracilis* Borradaile, 1915]

*Urocaridella gracilis* Borradaile, 1915: 210. [Maldives Islands]

*Urocaridella urocaridella*.—Chace & Bruce, 1993: 42.—Li et al., 2007: 169, fig. 72.

**Material examined.** — Miaoli County; 20.03.2002; 1 ♂, pochl. 7.0 mm; NTOU. Kaohsiung County; 36 m; 29.11.2003; 7 ♂♂, pochl. 5.0-7.3 mm; 2 ovigerous ♀♀, pochl. 6.9, 7.0 mm; 8 ♀♀, pochl. 5.4-7.1 mm; NTOU.

**Diagnosis.** — Rostrum with 1-3+3-5+2/10-12 teeth, excluding epigastric tooth on carapace; carapace with branchiostegal spine removed from margin by about length of spine; mandible with well developed 2-segmented palp; first pereopod with fingers distinctly longer than palm, palm subequal or slightly longer than carpus; second pereopod with fingers 1.5 times as long as palm, palm distinctly longer than carpus; third pereopod with propodus less than three times (but see remarks) as long as dactyl; third abdominal somite with dorsal profile nearly subrectangular, 5th abdominal pleuron with small acute tooth posteroventral tooth; posterior margin of telson acutely triangular, inner pair of posterior marginal setae slender, plumose.

**Size.** — Maximum postorbital carapace length probably about 5 mm (Chace & Bruce, 1993); 7.3 mm (present material).

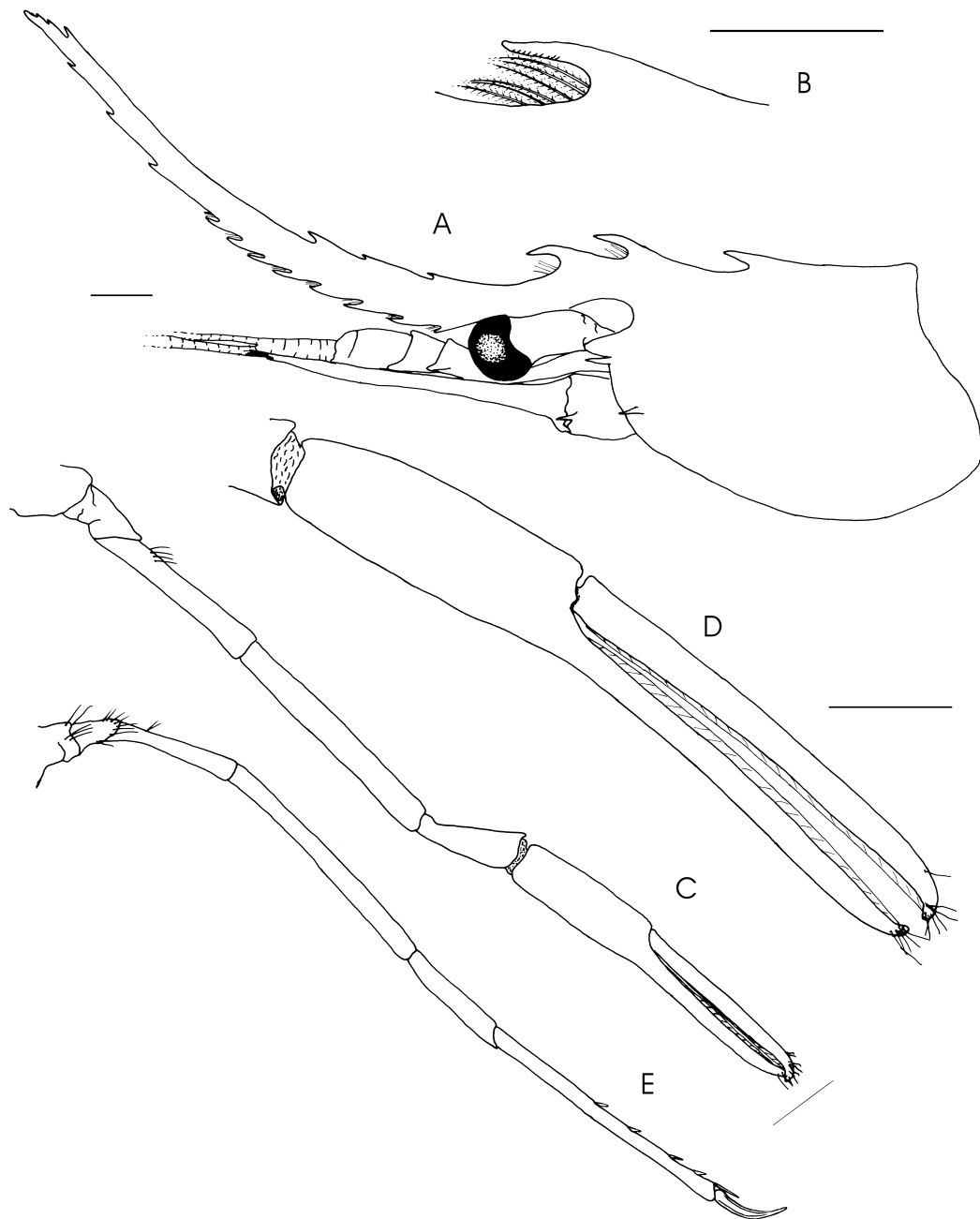
**Colouration.** — Unknown

**Habitat.** — Marine to a depth of 125 m (Bruce, 1990).

**Distribution.** — Maldives Islands, northeastern India, Andaman Islands, Mergui Archipelago, Indonesia, China, New Caledonia (Li et al., 2004). The first records from Taiwan are given here.

**Remarks.** — The present specimens show some notable differences between published descriptions (Holthuis, 1950; Chace & Bruce, 1993; Li et al., 2004). Chace and Bruce (1993) state that the maximum postorbital carapace length is probably about 5 mm whereas the specimens examined here are up to 7.3 mm. In addition the proportions of the propodi to the dactyli of the third to fifth pereopods differ from published descriptions. *Urocaridella urocaridella* is said to have the propodus of the third pereopod less than three times as long as the dactylus whereas it is greater than three times as long (3.3-3.6 times) in the present material; the propodus of the fourth





**Figure 17.** *Urocaridella urocaridella* (Holthuis, 1950): A, B, male (pocl. 5.6 mm – NTOU); Kaohsiung County; C-E, male (pocl. 7.0 mm – NTOU); Miaoli. A. carapace, left lateral view; B. second basal tooth, left lateral view; C. right second pereiopod, lateral view; D. same, chela, mesial view; E. right fifth pereiopod, mesial view. Scale bars indicate 1.0 mm.

and fifth pereopods is described as being less than four times as long as the dactylus whereas it is four times as long as the dactylus in the Taiwanese material. Finally, the third abdominal somite has a weak constriction such that it forms a small hump. This hump is not as pronounced as that in *U. antonbruunii* described above but it should not be present in *U. urocaridella*. These differences may in part be attributed to the larger size of the specimens examined here but the true taxonomic significance of these features requires investigation.

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## **Chapter 2: Systematics of *Palaemon***

Regional scale speciation reveals multiple invasions of freshwater in Palaemoninae  
(Decapoda).

[Published in: *Zoologica Scripta* 41(3): 293–306 (2012)].





**Regional scale speciation reveals multiple invasions of freshwater in  
Palaemoninae (Decapoda)**

**Abstract**

The generic level, systematic relationship in Palaemoninae was inferred from analyses based on the mitochondrial 16SrRNA and nuclear Histone (H3) genes, primarily focussed on the genera *Palaemon* and *Palaemonetes*, as previous morphological and molecular studies indicated potential paraphyly in some genera. *Palaemonetes*, *Exopalaemon*, *Coutierella* and certain *Palaemon* recover as a strongly supported monophyletic clade, but with the exception of *Palaemon concinnus*, *P. pandaliformis* and *P. gracilis*. Within this clade, six major clades are identified with geographic relationships appearing stronger than generic relationships. The data strongly suggest that *Palaemon*, *Palaemonetes*, *Exopalaemon* and *Coutierella* are synonymous and that the morphological characters currently used to define these genera require re-evaluation. Freshwater species are not closely related to each other, but instead group with geographically close marine species, suggesting multiple invasions of freshwater by physiologically plastic ancestors rather than a single colonisation event with subsequent speciation.

**Introduction**

The caridean shrimp family Palaemonidae contains two currently recognised subfamilies: the morphologically diverse and strictly marine Pontoniinae Kingsley, 1879 and the Palaemoninae Rafinesque, 1815, which are the subject of this study. The Palaemoninae are found in marine, brackish and fresh water in tropical and temperate regions, and are all free-living with a relatively conservative gross morphology. The Palaemoninae contains 21 recognised genera (De Grave & Fransen, 2011), numerically dominated by *Macrobrachium* Spence Bate, 1868, that are restricted to fresh and brackish water. *Macrobrachium* have been intensively studied due to their diversity in easily accessible habitats and have been the subject of many molecular phylogenetic studies (e.g. Murphy & Austin, 2003, 2004, 2005; Liu et al., 2007; Chen et al., 2009; Wowor et al., 2009; Pileggi & Mantelatto, 2010). The second and third most speciose genera in the subfamily are *Palaemon* Weber, 1795

and *Palaemonetes* Heller, 1869, with 41 and 31 species respectively (De Grave & Fransen, 2011). These have worldwide distributions in both tropical and temperate regions and have representatives in marine, brackish and freshwaters, with two species of *Palaemon* reported from all three water types. Both *Palaemon* and *Palaemonetes* are well represented in the literature across many scientific disciplines and several molecular studies have been conducted at the population level within certain species of each genus (e.g. Berglund & Lagercrantz, 1983; Fidhiany et al., 1988; Teske et al., 2007; Reuschel et al., 2010; Chaves-Campos et al., 2011). However, neither genus has been subjected to the same level of phylogenetic analysis as *Macrobrachium*. The only in-depth phylogenetic study of these genera to date is the morphological cladistic study of Pereira (1997). Despite this limited treatment, previous studies have hinted at probable paraphyly in these genera (Pereira, 1997; Murphy & Austin, 2004). In contrast, within *Palaemonetes*, Strenth (1976) suggested that the majority of the freshwater species formed a strongly supported monophyletic clade based on the morphology of the larval antennal scale. A thorough molecular treatment is thus long overdue.

As many Palaemoninae are highly conservative in morphological features (Walker & Poore, 2003; Short, 2004) problems exist in delineating genera. The current genus-level classification of the Palaemoninae relies heavily on a differential combination of a small number of characters, prime amongst which is the presence or absence of the mandibular palp. *Palaemonetes* is currently separated from *Palaemon* solely through the absence of a mandibular palp versus presence in the latter genus. This character is widely used as a diagnostic character in numerous genera across several caridean families, although invariably in combination with several other characters. Early on, Kemp (1925) suggested that a single negative character may not be seen to support an entire genus and Bruce (1989) concluded that the presence or absence of a mandibular palp as the single difference does not seem to be an adequate character on which to separate genera. Furthermore, variability in the presence or absence of the mandibular palp as well as the number of segments has been demonstrated in species of each genus, most notably by Fujino and Miyake (1968), Chace (1972), Bray (1976) and Carvacho (1979). Despite this inherent variability in the only diagnostic morphological character, *Palaemon* and *Palaemonetes* have been maintained as separate genera in all recent classifications of Decapoda (e.g. De Grave & Fransen, 2011).

Due to the conflicting evidence from these previous studies, the present study was conceived to elucidate the relationship between *Palaemon* and *Palaemonetes*, including related Palaemoninae genera, effectively testing their reciprocal monophyly.

## Material and Methods

### *Taxon sampling*

Thirty one species of *Palaemonetes* (hereafter abbreviated to *Pt.*) and 41 species of *Palaemon* (hereafter abbreviated to *P.*) are currently recognised. Of these, specimens of 11 (35%) species of *Palaemonetes* and 25 (61%) species of *Palaemon* were sequenced for the present study, covering a wide geographical range and a variety of habitats and lifestyles. Additional sequences were obtained from GenBank. In some cases, multiple specimens of a species from different locations were sequenced or additional GenBank sequences obtained, and, where these sequences were clearly divergent, indicating possible cryptic species, we have included more than one exemplar in the final analyses (designated by different numbers).

Other Palaemoninae included in this study comprised two species of *Macrobrachium*, four species of *Exopalaemon*, and one species each of *Brachycarpus*, *Coutierella*, *Creaseria*, *Cryphiops*, *Leptocarpus*, *Nematopalaemon*, *Leander* and *Urocaridella*. Two species of two genera belonging to the Kakaducarididae were also included and the tree was rooted with *Anchistioides antiguensis* (Schmitt, 1924) (Anchistioididae).

Details of the species used in the analysis can be found in Table 1. All material newly sequenced for this study is accessioned in the Zoological Collections of Oxford Museum of Natural History (OUMNH-ZC). DNA samples were extracted from fifth pleopods, where possible, to avoid damage of any taxonomically informative morphological characters.

**Table 1.** Palaemonid species used in the analyses, including H3 and 16S GenBank accession numbers and provenance of specimens.

NTOU = National Taiwanese Ocean University; OUMNH-ZC = Oxford Museum of Natural History Zoological Collections.

Taxon	Museum Accession Number	Sampling Location	Habitat	GenBank Accession Number		GenBank Reference
				16S	H3	
<i>Anchistoides antiguensis</i> (Schmitt, 1924)	-	Caribbean	Marine	EU920911	EU921043	Toon <i>et al.</i> (2009)
<i>Brachycarpus biunguiculatus</i> (Lucas, 1846)	OUMNH-ZC 2006-10-0011	Punto Vargas, Costa Rica	Marine	JN674323	JN674391	
<i>Coutierella tonkinensis</i> Sollaund, 1914	OUMNH-ZC 2003-07-0001	Mai Po, Hong Kong	Brackish	JN674324	EU921053	Toon <i>et al.</i> (2009)
<i>Creaseria morleyi</i> (Creaser, 1936)	-	Americas	Freshwater	EU449001	DQ079671	Porter <i>et al.</i> (2005)
<i>Cryphiops (Cryphiops) caementarius</i> (Molina, 1782)	-	Americas	Freshwater	DQ079711	DQ079672	Porter <i>et al.</i> (2005)
<i>Exopalaemon annandalei</i> (Kemp, 1917)	-	Asia	Freshwater	DQ647670	-	Yang & Chen (unpub)
<i>Exopalaemon carinicauda</i> (Holthuis, 1950)	OUMNH-ZC 2009-16 0005	Mai Poi, Hong Kong	Brackish	JN674325	JN674393	
<i>Exopalaemon modestus</i> (Heller, 1862)	-	Taiwan	Freshwater	EU493144	-	Chen <i>et al.</i> (2009)
<i>Exopalaemon orientis</i> (Holthuis, 1950)	OUMNH-ZC 2010-02-0078	Pingtung County, Taiwan	Marine	JN674326	JN674387	
<i>Kakaducaris glabra</i> Bruce, 1993	-	Australia	Freshwater	EF588318	EU249461	Page <i>et al.</i> (2008)
<i>Leander tenuicornis</i> (Say, 1818)	OUMNH-ZC 2009-05-0004	Vaca Key, Florida, USA	Marine	JN674327	JN674388	
<i>Leptocarpus potamiscus</i> (Kemp, 1917)	OUMNH-ZC 2009-03-0006	Sungai Petani river, Malaysia	Fresh & Brackish	JN674328	JN674392	
<i>Leptopalaemon gagadju</i> Bruce, 1993	-	Australia	Freshwater	EF588310	EU249459	Page <i>et al.</i> (2008)
<i>Macrobrachium australiense</i> Holthuis, 1950	-	Australia	Freshwater	EF588317	EU249460	Page <i>et al.</i> (2008)
<i>Macrobrachium lar</i> (Fabricius, 1798)	-	French Polynesia	Freshwater	EF588316	EU249462	Page <i>et al.</i> (2008)
<i>Nematopalaemon tenuipes</i> (Henderson, 1893)	NTOU	Pingtung County, Taiwan	Marine	JN674329	JN674382	
<i>Palaemon adspersus</i> Rathke, 1837	OUMNH-ZC 2004-16-0001	Algarve, Portugal	Marine	JN674330	JN674360	
<i>Palaemon affinis</i> H. Milne Edwards, 1837	OUMNH-ZC 2004-12-0002	Mission Bay, New Zealand	Marine	-	JN674379	
<i>Palaemon concinnus</i> Dana, 1852	OUMNH-ZC 2010-02-0079	Pingtung County, Taiwan	Marine, Brackish and Freshwater	JN674331	JN674363	
<i>Palaemon debilis</i> Dana, 1852	-	Indonesia	Marine, Brackish and Freshwater	FM986647	FM958134	Wowor <i>et al.</i> (2009)
<i>Palaemon debilis</i> Dana, 1852	OUMNH-ZC 2009-21-0020	Wailoa, Hawaii	Marine, Brackish and Freshwater	JN674332	JN674375	
<i>Palaemon dolospinus</i> Walker & Poore, 2003	OUMNH-ZC 2009-25-0002	Port Phillip Bay, Victoria, Australia	Marine	JN674333	JN674389	
<i>Palaemon elegans</i> Rathke, 1837	OUMNH-ZC 2010-02-0004	The Fleet, England	Marine	EU868696	JN674378	Bracken <i>et al.</i> (2009)
<i>Palaemon floridanus</i> Chace, 1942	-	USA	Marine	GQ227820	-	Baeza (2010)
<i>Palaemon gracilis</i> (Smith, 1871)	OUMNH-ZC 2009-18-0016	Miraflores Locks, Panama	Brackish	JN674334	JN674362	
<i>Palaemon guangdongensis</i> Liu, Liang & Yan, 1990	OUMNH-ZC 2009-16-0004	Pearl River mouth, south China	Marine	JN674335	JN674394	
<i>Palaemon intermedius</i> (Stimpson, 1860)	OUMNH-ZC 2009-09-0004	Loders Creek, Gold Coast, Australia	Marine	JN674336	JN674361	
<i>Palaemon litoreus</i> (McCulloch, 1909)	OUMNH-ZC 2004-14-0019	Rottneest Island, Western Australia	Marine	JN674337	JN674369	
<i>Palaemon longirostris</i> H. Milne Edwards, 1837	OUMNH-ZC 2009-07-0003	River Thames, England	Brackish	-	JN674386	
<i>Palaemon longirostris</i> H. Milne Edwards, 1837	OUMNH-ZC 2001-09-0052	River Thames, England	Brackish	JN674338	-	
<i>Palaemon macrodactylus</i> Rathbun, 1902	OUMNH-ZC 2001-09-0053	River Thames, England	Brackish	DQ642875	JN674385	Mitsubishi <i>et al.</i> (2007)
<i>Palaemon northropi</i> (Rankin, 1898)	OUMNH-ZC 2008-14-0129	Bocas Del Toro, Panama	Marine	-	JN674380	
<i>Palaemon ortmanni</i> Rathbun, 1902	OUMNH-ZC 2003-06-0002	Seto Inland Sea, Japan	Marine	JN674339	-	
<i>Palaemon pacificus</i> (Stimpson, 1860)	OUMNH-ZC 2008-18-0024	Keelung Ho-Ping Island Park, Taiwan	Marine	JN674340	FM958135	Wowor <i>et al.</i> (2009)
<i>Palaemon pandaliformis</i> (Stimpson, 1871)	OUMNH-ZC 2008-14-0020	Rio Oeste, Panama	Freshwater	JN674341	JN674364	
<i>Palaemon paucidens</i> De Haan, 1844	OUMNH-ZC 2003-06-0003	Utanogawa River, Japan	Marine, Brackish and Freshwater	JN674342	JN674383	
<i>Palaemon peringueyi</i> (Stebbing, 1915)	OUMNH-ZC 2003-09-0001	Kariega River Estuary, South Africa	Marine	JN674343	JN674365	
<i>Palaemon ritteri</i> Holmes, 1895	OUMNH-ZC 2009-18-0011	Coiba, Panama	Marine	JN674344	JN674367	
<i>Palaemon semmelinki</i> (De Man, 1881)	-	Sturt Island (Sialowa), P.N.G.	Marine	JN674345	JN674400	
<i>Palaemon serenus</i> Heller, 1862	OUMNH-ZC 2009-09-0011	Wellington Point, Queensland, Australia	Marine	JN674346	JN674368	
<i>Palaemon serratus</i> (Pennant, 1777)	OUMNH-ZC 2010-02-0002	River Orwell, England	Marine	-	JN674377	
<i>Palaemon serrifer</i> (Stimpson, 1860)	OUMNH-ZC 2005-04-0001	Busan, South Korea	Marine	JN674347	JN674366	

Table 1. cont.

Taxon	Museum Accession Number	Sampling Location	Habitat	GenBank Accession Number		GenBank Reference
				16S	H3	
<i>Palaemon serrifer</i> (Stimpson, 1860)	OUMNH-ZC 2004-13-0004	Labrador Beach, Singapore	Marine	-	JN674370	
<i>Palaemon serrifer</i> (Stimpson, 1860)	OUMNH-ZC 2010-02-0077	Pingtung County, Taiwan	Marine	JN674348	JN674373	
<i>Palaemon xiphias</i> Risso, 1816	OUMNH-ZC 2003-02-0001	Blanes, Spain	Marine	-	JN674376	
<i>Palaemon xiphias</i> Risso, 1816	OUMNH-ZC 2010-02-0001	Ebro Delta, Spain	Marine	JN674349	-	
<i>Palaemonetes antennarius</i> H. Milne Edwards, 1837	OUMNH-ZC 2003-03-0002	Epta Piges River, Rhodos Island, Greece	Freshwater	JN674350	JN674395	
<i>Palaemonetes argentinus</i> Nobili, 1901	OUMNH-ZC 2002-03-0001	Mar del Plata, Argentina	Freshwater	JN674351	JN674397	
<i>Palaemonetes atrinubes</i> Bray, 1976	OUMNH-ZC 2009-21-0012	Couran Cove, Queensland, Australia	Marine	JN674352	JN674399	
<i>Palaemonetes atrinubes</i> Bray, 1976	-	Australia	Marine	AF439520	-	Murphy & Austin (2003)
<i>Palaemonetes australis</i> Dakin, 1915	OUMNH-ZC 2009-21-0010	Blackwood River, Western Australia	Freshwater	JN674353	JN674401	
<i>Palaemonetes intermedius</i> Holthuis, 1949	OUMNH-ZC 2002-14-0001	Manatee Bay, Florida, USA	Brackish	JN674354	JN674396	
<i>Palaemonetes paludosus</i> (Gibbes, 1850)	OUMNH-ZC 2004-14-0002	Jefferson County, Florida, USA	Freshwater	-	JN674381	
<i>Palaemonetes pugio</i> Holthuis, 1949	OUMNH-ZC 2009-07-0005	Ocean Springs, Mississippi, USA	Brackish	JN674355	JN674371	
<i>Palaemonetes schmitti</i> Holthuis, 1950	OUMNH-ZC 2002-18-0001	Gulf of Nicoya, Pacific coast, Costa Rica	Marine	JN674356	JN674390	
<i>Palaemonetes sinensis</i> (Sollaud, 1911)	OUMNH-ZC 2003-06-0005	Bait store, Japan	Freshwater	-	JN674384	
<i>Palaemonetes varians</i> (Leach, 1813)	OUMNH-ZC 2009-07-0009	River Blackwater, England	Brackish	JN674357	JN674374	
<i>Palaemonetes vulgaris</i> (Say, 1818)	OUMNH-ZC 2009-07-0006	Ocean Springs, Mississippi, USA	Marine	JN674358	JN674372	
<i>Urocaridella antonbruunii</i> (Bruce, 1967)	OUMNH-ZC 2010-02-0073	Kenting, Taiwan	Marine	JN674359	JN674398	

### *Molecular data retrieval*

Total genomic DNA was extracted and gene fragments sequenced in both directions as per Page et al. (2008). Two genes were sequenced, the mitochondrial, ribosomal gene 16SrRNA (16S) and a nuclear gene, protein coding Histone (H3). These markers were selected primarily because they give resolution at species and generic levels, which is the focus of this study. The 16S rRNA gene has both fast and slowly evolving regions and, therefore, can provide useful information across a broad taxonomic spectrum (Murphy & Austin, 2004). As a nuclear gene, H3 is more conserved and is likely to provide resolution at deeper levels than 16S. Forward primers for the 16S polymerase chain reaction were 16S-F-Car (von Rintelen et al., 2007) or 16Sar (Palumbi et al., 1991), and reverse primers 16S-R-Car or 16S-R-Car1 (von Rintelen et al., 2007) or 16Sbr (Palumbi et al., 1991). Primers for Histone were H3-F and H3-R (Colgan et al., 1998).

### *Phylogenetic analysis*

Both genes were analysed separately and in a combined analysis. The datasets were aligned with Sequencher version 4.1.1 b1 (Gene Codes Corporation) at default settings. The best-fit models of molecular evolution (Akaike's Information Criterion) were selected separately for both gene regions within each dataset and for the combined dataset as a whole, using Modeltest version 3.06 (Posada & Crandall, 1998) in PAUP\* version 4.0 b10 (Swofford, 2002). We carried out two different forms of phylogenetic inference on the combined dataset; maximum likelihood analysis (PHYML version 2.4.4; Guindon & Gascuel, 2003) and parsimony (TNT version 1.1; Goloboff et al., 2008) and both were bootstrapped 1000 times.

## **Results**

### *Sequences*

We obtained 37 new 16SrRNA sequences and 42 new H3 sequences (Table 1), a further 14 16S and 10 H3 Genbank sequences were included. Five species were only represented by a 16S sequence: *Exopalaemon annandalei*, *E. modestus*,

*Palaemon floridanus*, *P. ortmanni*, and *Palaemonetes atrinubes* 1, whilst six only by H3: *P. affinis*, *P. northropi*, *P. serratus*, *P. serrifer* 2, *Pt. paludosus* and *Pt. sinensis*.

The H3 sequences were 328 base pairs (bp) and the 16S dataset was 418bp (aligned) and corresponds to positions 11365 - 11764 of the *Macrobrachium dacqueti* (Sunier, 1925) mitochondrial genome (accession number NC006880, Miller et al., 2005).

#### *Phylogenetic analyses*

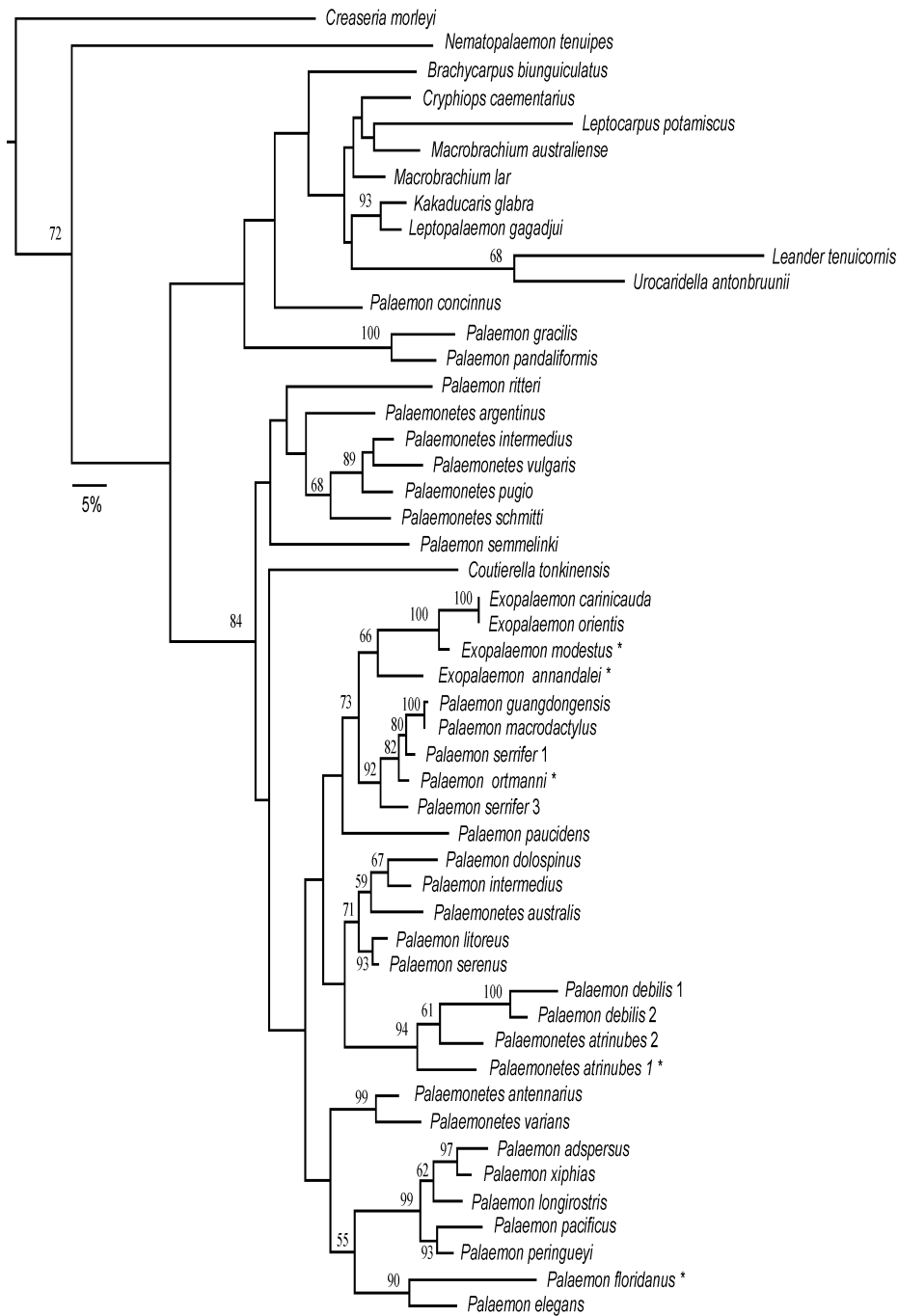
For the combined and 16S phylogenetic analyses, Modeltest selected a General Time Reversible model of evolution, and a Hasegawa, Kishino and Yano model for the H3 analysis. Chi-square tests of homogeneity of base frequencies across ingroup taxa found no significant differences ( $P > 0.99$ ). PHYML recovered a single phylogenetic tree for each dataset (combined log score = -8917.50; 16S = -6587.95; H3 = -2686.67). TNT recovered 16 equally parsimonious topologies of 1851 steps for the combined dataset.

The maximum likelihood phylograms produced for 16S (Figure 1), H3 (Figure 2) and the combined analysis (Figure 3) are given here. Most clades were recovered with high bootstrap support, but many deeper nodes were poorly supported. Only bootstrap values >50% are shown on the trees.

The well-supported clades obtained in the individual gene trees were very similar (Figure 1 and Figure 2) but some differences were observed in the topology of the poorly supported branches.

#### *Analyses of the major clades*

In all three analyses *Palaemonetes*, *Exopalaemon*, *Coutierella* and certain *Palaemon*, recover as a strongly supported single monophyletic clade (the “*Palaemon*” Clade, Figure 3) with the exception of *Palaemon concinnus*, *P. gracilis* and *P. pandaliformis*. *Palaemon gracilis* and *P. pandaliformis* are closely related to each other and recover with strong support (Figure 3) whilst *P. concinnus* has no clear affinity to any of the taxa included in our analysis.



**Figure 1.** Maximum likelihood phylogram of 16S analysis. Maximum likelihood bootstrap values are given; only values >50% are shown. \* = 16S only, no H3.

Within the “*Palaemon*” clade, six smaller clades can be identified from the combined analysis (Figure 3), most of which broadly reflect the current geographic distribution of the constituent species. For ease of reference these clades are referred to by the current geographic region of the majority of their constituent species.



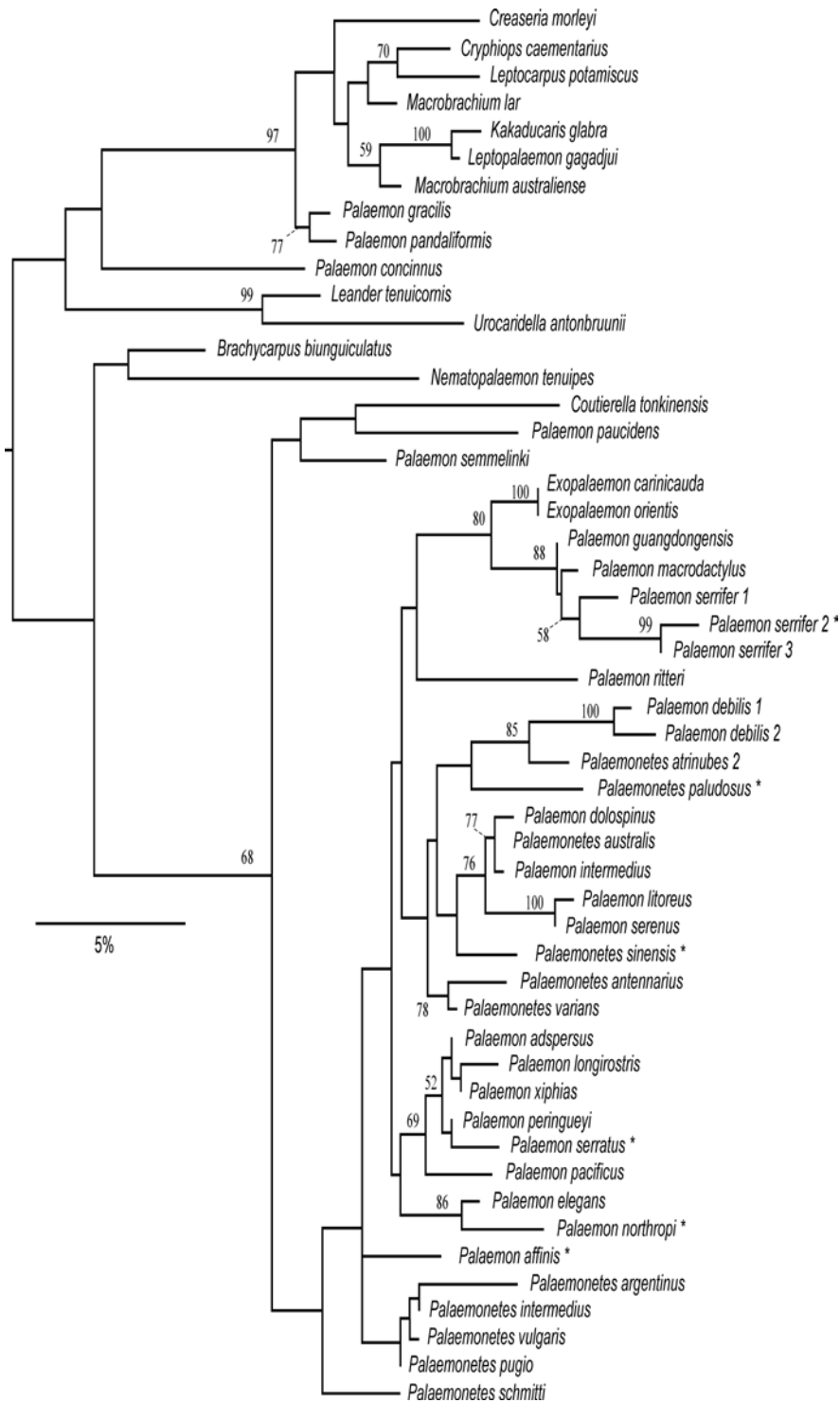
The Asia 1 Clade comprises just two species: *Coutierella tonkinensis* and *Palaemon paucidens* but has low support compared with many of the other clades in this analysis (Figure 3) and was not retrieved as monophyletic in the 16S analysis (Figure 1).

The American Clade comprises six species from both North and South America, distributed on both sides of the continent in marine, brackish and fresh water. The relationship between *Pt. intermedius*, *Pt. pugio*, *Pt. vulgaris* and *Pt. schmitti* is well supported, whilst the inclusion of *P. ritteri* and *Pt. argentinus* in this clade is less well supported (Figure 3). The American Clade does not recover as monophyletic in the H3 analysis (Figure 2) due to the exclusion of *P. ritteri*. *Palaemonetes paludosus*, a freshwater species from the Americas, has no close affinity to the American Clade based on the H3 analysis (Figure 2) and is of uncertain placement.

Eight currently recognised species of *Palaemon* and *Exopalaemon* are included in the Asia 2 Clade. However, high levels of genetic divergence were noted amongst material identified as *P. serrifer*, indicating the existence of three probable cryptic species. Conversely, material identified as *Exopalaemon carinicauda* and *E. orientis* had very low genetic diversity suggesting that they are very recently diverged or possibly represent conspecific ecotypes. *Palaemon ortmanni*, *Exopalaemon modestus* and *E. annandalei* were represented by 16S sequences only whilst *P. serrifer* 2 from Singapore was only represented in the H3 tree but their inclusion in this clade is well supported. Within the Asia 2 Clade, *Exopalaemon* spp. recover as a strongly supported monophyletic clade (Figure 3). *Palaemon semmelinki*, which is found in south Asia, is of uncertain placement in our analyses but does not have a strong relationship to either Asian clade (Figure 3). It is the only species of the “*Palaemon*” Clade not to have a well supported relationship to any of the six clades identified in the combined analysis. Likewise, *Palaemonetes sinensis* does not appear closely related to either the Asia 1 or Asia 2 Clade based on the H3 tree (Figure 2). These two species may represent further Asian lineages.

The five constituent species of the Australian Clade (*P. dolospinus*, *P. intermedius*, *P. litoreus*, *P. serenus*, and *Pt. australis*) form a well supported group (Figure 3). Another Australian species, *Pt. atrinubes*, does not form part of the Australian clade, as already speculated in the original description of the species (Bray, 1976) and *Palaemon affinis* from New Zealand, represented by a H3 sequence only,

was of uncertain placement in our analysis but does not seem to have a strong affinity to the Australian species (Figure 2).

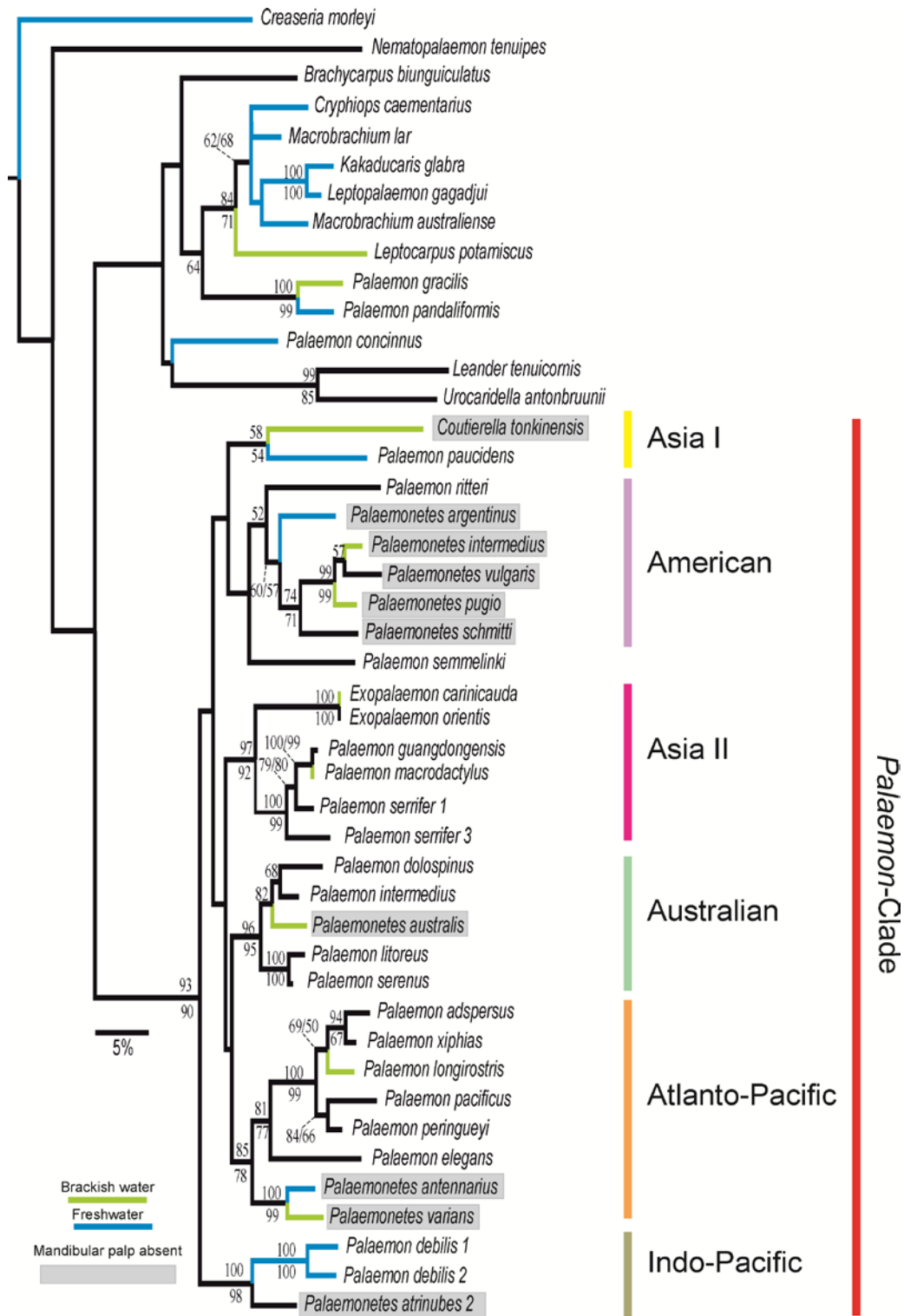


**Figure 2.** Maximum likelihood phylogram of H3 analysis. Maximum likelihood bootstrap values are given; only values >50% are shown. \* = H3 only, no 16S.

The Atlanto-Pacific Clade comprises three smaller clades. The European *Palaemon adspersus* (the type species of *Palaemon*), *P. longirostris*, *P. serratus* and *P. xiphias* form a well supported clade together with the South African *P. peringueyi* and the Indo-Pacific *P. pacificus*. *Palaemon elegans* is excluded from the clade containing the other European species and instead forms a clade with the western Atlantic species *P. floridanus* (Figure 1) and *P. northropi* (Figure 2). A strong relationship between the two European species of *Palaemonetes* included in our analysis, *Pt. varians* (the type species of *Palaemonetes*) and *Pt. antennarius*, is demonstrated but their relationship to the other species of the Atlanto-Pacific clade is less well supported (Figure 3).

*Palaemon debilis* and *Palaemonetes atrinubes* form a well supported clade, the Indo-Pacific Clade, in all analyses (Figures 1-3). Although this clade contains two named species, *Palaemon debilis* and *Pt. atrinubes*, sequences for both of these species showed high levels of divergence and the existence of cryptic species in both taxa is postulated.

*Kakaducaris glabra* and *Leptopalaemon gagadjui* (family Kakaducarididae) form a strongly supported clade nested within *Macrobrachium*. Amongst the other included Palaemoninae, *Cryphiops (Cryphiops) caementarius* forms a well supported clade with *Macrobrachium*, *Leptocarpus potamiscus* and the kakaducarid genera; *Urocaridella antonbruunii* forms a well supported clade with *Leander tenuicornis*, however the long branch-length indicates that the relationship between these species is not particularly close; whilst *Nematopalaemon tenuipes*, *Creaseria morleyi* and *Brachycarpus biunguiculatus* have no obvious affinities with any other outgroup taxa in the combined tree (Figure 3).



**Figure 3.** Maximum likelihood phylogram of combined analysis. Blue lineages are species occurring in freshwater, green are brackish water lineages and black are marine lineages. Shaded species lack a mandibular palp. Maximum likelihood (above line) and parsimony bootstrap (below line) values are given; only values >50% are shown.

## Discussion

### *Systematic implications*

The present analyses constitute the most comprehensive molecular phylogeny to date of Palaemoninae at the generic level, as well for *Palaemon* and *Palaemonetes* at species level, with a reasonably robust taxon sampling and utilising both mitochondrial and nuclear markers giving good resolution at both species and generic level. This approach has revealed several interesting patterns with potential implications for the current generic classification of the Palaemoninae; 1) most *Palaemon*, *Palaemonetes*, *Coutierella* and *Exopalaemon* form a well supported monophyletic clade in all analyses (the “*Palaemon*” Clade); 2) *Palaemon concinnus*, *P. gracilis* and *P. pandaliformis* are excluded from the “*Palaemon*” Clade; 3) within this large “*Palaemon*” Clade, six smaller clades can be identified, largely reflecting current distribution of constituent taxa, with two, or possibly more, separate clades identified from Asia; 4) *Exopalaemon* constitute a monophyletic clade in all trees nested within the Asia 2 Clade; 5) *Urocaridella* appears as a sister taxon to *Leander*; 6) *Cryphiops* (*Cryphiops*) *caementarius* forms a clade with *Macrobrachium* with strong support, in agreement with the findings of Pereira (1997) and Pileggi and Mantelatto (2010); 7) the kakaducarid genera *Leptopalaemon* and *Kakaducaris* appear allied to *Macrobrachium* and therefore nested within the Palaemoninae supporting the conclusions of Page et al. (2008) and Bracken et al. (2009).

The main implication of our analyses is that *Palaemon*, *Palaemonetes*, *Exopalaemon* and *Coutierella* do not form reciprocal monophyletic clades supporting their current separate generic level status. Instead they form a clade of mixed genera that, to an extent, reflects the geographic distributions of the species rather than their generic affiliation. The occurrence of the type species of both *Palaemon* and *Palaemonetes* (*P. adspersus* and *Pt. varians*, respectively) in the Atlanto-Pacific Clade supports the likely synonymy of these genera, which has previously been suggested by other workers (Kemp, 1925; Chace, 1972; Bray, 1976; Pereira, 1997; Knowlton & Vargo, 2004). This is in contrast to the morphological phylogeny conducted by Pereira (1997) which differs in that the two genera are not as intermixed, but nevertheless largely integrate with each other.

*Palaemon concinnus*, *P. gracilis* and *P. pandaliformis* are excluded from the “*Palaemon*” Clade in our analysis. *Palaemon gracilis* and *P. pandaliformis* are part of a morphologically homogeneous group in reduced salinity and freshwater in Central America. The current analysis confirms the strong relationship between these species but places them outside of *Palaemon* and closer to *Macrobrachium*. Morphologically, these species conform to the most recent definition of *Palaemon* (Walker & Poore, 2003) which implies possible convergent evolution in the expression of certain characters, especially the placement of the carapace spine in a branchiostegal position. The morphological cladistic analysis of Pereira (1997) also placed these species in a monophyletic clade but within *Palaemon*, as a sister group to *Exopalaemon orientis*, *Nematopalaemon schmitti* and *Leptocarpus potamiscus*. *Palaemon concinnus* is also placed outside of *Palaemon* in our analysis but in Pereira’s (1997) study it was included in a curious assemblage of *Palaemon* species comprising two Asian species, one widespread Indo-Pacific species, one eastern Pacific species and two European species. As currently classified, *P. concinnus* is unique within the genus in possessing a rudimentary appendix on the endopod of the first pleopod of males. This character is also found in several other genera within the subfamily (*Leander*, *Brachycarpus*, *Leandrites* and *Urocaridella*). A morphological reappraisal of *P. concinnus*, as well as *P. pandaliformis* and *P. gracilis* to ascertain their generic affinities thus appears desirable.

In our data, species of *Exopalaemon* form a strongly supported monophyletic clade within the Asia 2 Clade. *Exopalaemon* was originally described as a subgenus of *Palaemon* by Holthuis (1950) but later afforded generic level status by Chace and Bruce (1993), characterised by having a strong basal crest to its rostrum. Within the subfamily, *Nematopalaemon* is the only other genus to possess a strongly crested rostrum, although several species of *Macrobrachium* are described as having a ‘somewhat-crested’ rostrum. Our data therefore suggest that *Exopalaemon* represents a derived clade of *Palaemon* in Asian waters. Recently, Baeza et al. (2009) and Baeza (2010) demonstrated the paraphyly of *Lysmata* Risso 1816 (Hippolytidae) caused by the inclusion of *Exhippolysmata* Stebbing 1915 (but see Fiedler et al., 2010). This result has striking parallels with the current analysis as *Exhippolysmata* is likewise currently separated from *Lysmata* by possessing a crested rostrum.

For many years *Coutierella tonkinensis* was included in *Palaemonetes* until Bruce (1989) re-established *Coutierella* as a monotypic genus with the diagnostic

features being a lack of a well developed pleurobranch on the fourth thoracic segment, the presence of feebly developed, distinctly sub-spatulate chelae on the second pereopods and the presence of three or more pairs of spines on the posterior margin of the telson as well as several specialised features of the mouthparts. Here, *C. tonkinensis* with *P. paucidens* form the weakly supported Asia 1 Clade, casting doubt on the validity of the generic status of *Coutierella*.

Possible species complexes were indicated from our analyses centred around *Palaemon debilis*, *P. serrifer* and *Palaemonetes atrinubes*. In each case, genetic distance between exemplars was greater than that observed for some other well delineated species in the analyses. *Palaemon debilis* has previously been suspected of being a species complex on morphological grounds (De Grave & Al-Maslamani, 2006) and the current data lend weight to this suggestion, with a ~9.5% difference in the two 16SrRNA sequences. The specimens of *Pt. atrinubes* from western and eastern Australia differed by ~18.5% in the 16SrRNA data. Three species can be identified in the material identified as *P. serrifer* from Korea, Taiwan and Singapore, respectively. Previously, morphological variability has been noted in *P. serrifer* (e.g. Kubo, 1942; Holthuis, 1950; Nguyễn, 1992) and further analysis may reveal consistent morphological differences between these populations. The status of all these lineages should await a reappraisal of material of each species from across their respective geographic ranges. Reuschel et al. (2010) have also recently proposed cryptic species in the European *P. elegans* due to its high genetic diversity (2.5% in 16S and 8.7% in COI), but this species was only represented by a single exemplar in our analysis.

A combined morphological and molecular approach with greater taxon sampling and using more genes and novel morphological characters would be desirable to help resolve whether it is justifiable to synonymise *Palaemon*, *Palaemonetes*, *Exopalaemon* and *Coutierella* or create new genera to accommodate *P. concinnus*, *P. gracilis* and *P. pandaliformis*.

#### *The mandibular palp and its absence in Palaemonetes*

Within the Palaemoninae the mandibular palp is present in 13 of the 21 genera, absent in seven genera and variable in the remaining genus. The presence of a mandibular palp is generally considered the most primitive state in carideans. All

genera derived from the basal node in our analyses possess a mandibular palp (variable in *Urocaridella*) suggesting that this may be the plesiomorphic condition in Palaemoninae.

The presence of a mandibular palp is the sole character currently used to differentiate the genera *Palaemon* and *Palaemonetes*. This, however, only holds true for the adult form. A review of descriptions of larval Palaemoninae reveals that the mandibular palp is absent in all larval stages and Knowlton and Vargo (2004) concluded that the larval development of *Palaemon* and *Palaemonetes* are so similar that the two genera are extremely difficult to separate as larvae. Although Gore (1985) described the appearance of a mandibular palp as part of the normal pattern of larval development in decapods, in Palaemoninae the palp develops over a series of moults in juveniles rather than in the larval stages (Lewis & Ward, 1965; Pillai, 1973; Bray, 1976; Walker & Poore, 2003) coinciding with the development of sexual characters (appendix masculina in males and ovaries in females; Bray, 1976; pers. obs.). The lack of reciprocal monophyly of *Palaemon* and *Palaemonetes* demonstrated here strongly indicates that the absence of, or rather failure to gain, a mandibular palp in *Palaemonetes* cannot be regarded as a synapomorphy, but rather as a homoplastic character state. Species that lack a mandibular palp are found in five of the clades identified in these analyses plus two further species in the H3 only analysis (Figures 2-3). Why it is absent in some species poses the question of its function and whether its absence can be attributed to differences in life style, habitat or ecology of the animals. Although the mandibular palp is found in many caridean genera, it has received little attention in terms of its functionality. A logical conclusion may be that it is used during feeding but Borradaile (1917) stated that it was not used in food manipulation in *Palaemon serratus* and probably had a sensory function, although limited as it is absent in so many species (i.e. those species currently assigned to *Palaemonetes*). In contrast, Bauer (2004) suggested that the palp may be used in cleaning of the mandibles. There seems to be little difference in feeding mechanism and diet between species that have a palp or lack one, based on the limited available studies (Forster, 1951a, b; Sitts & Knight, 1979; Siegfried, 1982; Guerao, 1995; Janas & Barańska, 2008). A feeding-related function would potentially suggest a dietary shift between small juveniles and adults, evidence for which is lacking. Garm (2004) observed that the palp of *Palaemon adspersus* was not seen to move independently of the mandible, nor did it have prey contact, but when the



mandibles close it sweeps the lateral side of the labrum. This sweeping across the labrum is probably a grooming procedure (but not of the mandibles). More importantly, all mandibular palp setae are either mechano- or chemoreceptors (A. Garm, pers. comm.) implying a sensory function, possibly to sense the need for grooming.

Following this line of thought, the question of why the mandibular palp is absent mostly in freshwater species within the “*Palaemon*” Clade is raised. Whether the failure to develop a palp is also related to the adaptation to freshwater, as most *Palaemonetes* are freshwater animals, is not known. However, this would seem unlikely, as the palp is present in *Macrobrachium*, which is predominately a freshwater genus and has been retained in several freshwater species of *Palaemon*. However, both the segmentation and presence of the mandibular palp have been demonstrated to be variable characters in a number of previous studies (e.g. Fujino & Miyake, 1968; Chace, 1972), notably amongst species that tolerate reduced salinities.

#### *The invasion of freshwater*

Six species of *Palaemon* and 20 species of *Palaemonetes* are found in fresh water with five and six brackish water species respectively, whilst some species of *Palaemon* have been reported from all three water types. This apparent ecological split may, in part, have contributed to them being regarded as distinct genera.

The transition between marine and freshwater environments represents a huge evolutionary change for animals. Of those that have made the transition to fresh water, crustaceans are amongst the most frequently reported, possibly because the morphological and physiological traits of this group, such as the ability to reduce membrane permeability, promote the adaptation to freshwater environments (Lee & Bell, 1999). Decapods are well represented in fresh water with approximately 23% of known species inhabiting fresh water (Bond-Buckup et al., 2008; Crandall & Buhay, 2008; De Grave et al., 2008; Yeo et al., 2008).

The term ‘freshwater species’ is frequently used in the literature without definition but, unless defined, the term may be very inclusive and not very informative (Bogan, 2008). The definition of a freshwater animal remains controversial (Balian et al., 2008) and often problematic as in nature there is no neat dividing line between marine, brackish and fresh water. Rather, there is a continuous

gradation (Boxshall & Defaye, 2008) with many motile animals being diadromous. Whilst some workers have sought to employ salinity tolerance ranges in the definitions (e.g. Lee & Bell, 1999) and others have put life history traits of animals, such as abbreviation of larval development as a supplementary defining criterion (e.g. Cumberlidge & Ng, 2009), such definitions are often unworkable due to a paucity of information. As there is a gradient from species that spend all their lives in fresh water through diadromous species to those that spend all their lives in marine waters, we here use the term freshwater species to include all species that occur for all or part of their lives in fresh water (Lévêque et al., 2005) in all or part of their range.

Representatives of eight caridean shrimp families are found in fresh water, dominated by the Atyidae and Palaemonidae (De Grave et al., 2008). The subfamily Palaemoninae is widely believed to have radiated into fresh water from ancestral marine stock (e.g. Sollaud, 1923; Rabalais & Gore, 1985; Freire et al., 2003; Murphy & Austin, 2004) with the large genus *Macrobrachium* being essentially confined to fresh- and euryhaline water. Freire et al. (2003) and Augusto et al. (2009) hypothesise that freshwater palaemonid shrimp have taken a direct route via brackish waters, followed by penetration into freshwater habitats, with speciation either driven by separation of river basins by vicariant events or indicative of separate invasions of fresh water, as has been shown in atyid shrimps (Cook et al., 2006). Which of these processes has led to the present, disparate distribution of the freshwater species of Palaemoninae, particularly *Palaemonetes*, has remained unanswered. Laboratory studies on the salinity tolerance of the larvae of the freshwater species *Pt. kadiakensis* conducted by Strenth (1976) indicated that it has an inability to disperse over large oceanic stretches, supporting previous theories regarding the dispersal capabilities of freshwater animals. With the exception of *Pt. argentinus*, the nine American freshwater species of *Palaemonetes* (including *Calathaemon holthuisi*) recognised by Strenth (1976), as well as *Pt. antennarius* and *Pt. sinensis* from Europe and China respectively, were assumed to represent a monophyletic group based on antennal scale characteristics of the larvae. From this, it was theorised that freshwater *Palaemonetes* arose from one major colonisation event with dispersal between disparate regions occurring via land bridges or when land masses were closer together, and with subsequent radiation in fresh water but with possible limited polyphyly (i.e. that of *Pt. argentinus*). The paucity of species in certain regions was believed to be due to competitive exclusion by *Macrobrachium* or extinction of intermediate species

(Streth, 1976). The high morphological similarity of adults (Pereira, 1997) partially supports Streth's (1976) view that they represent a single invasion of freshwater with subsequent radiation. In contrast, we demonstrate a conflicting scenario and document the colonisation of fresh water in five of the major geographically defined clades, in *P. pandaliformis* and *P. concinnus* and a further three potential colonisation events being suggested by the separate 16S and H3 trees (*Pt. paludosus*, *Pt. sinensis*, *E. annandalei* and *E. modestus*). This indicates that a minimum of ten independent invasions of fresh water has occurred in species currently assigned to *Palaemon* or included in the “*Palaemon*” Clade and that species have independently evolved the ability to survive in fresh water in all major biogeographic regions and we can confidently discount Streth's (1976) single colonisation followed by radiation hypothesis. The numerous species of the “*Palaemon*” Clade occurring in marginal marine and brackish habitats indicates that the colonisation of freshwaters by this group may still be progressing.

The number of invasions demonstrated suggests that “*Palaemon*” species have significant potential over evolutionary time for such habitat transitions. This is supportive of Lee and Bell's (1999) observation that once the evolutionary innovation to invade freshwater arises in a clade, freshwater invasion appears to occur repeatedly. A review of the literature suggests that ten demonstrable independent invasions of freshwater within a single worldwide genus may be unprecedented. Although multiple invasions of freshwater have been demonstrated at higher taxonomic levels (e.g. freshwater genera within families) or smaller geographic scales (e.g. Bartsch, 1996; Boxshall & Jaume, 2000; Bogan, 2008; Strong et al., 2008; Väinölä et al., 2008; Wilson, 2008; Yeo et al., 2008), no other invertebrate genus seems to have achieved this number of independent invasions of freshwater.

The molecular evidence presented here casts serious doubt on the current generic classification of the Palaemoninae. In view of this, an in depth appraisal of the currently employed morphological characters is required, including the search for new characters. We also demonstrate multiple invasions of freshwater occurring on an unprecedented scale.

### Acknowledgements

Dr Anders Garm (University of Copenhagen) is thanked for interesting discussions on mandibular palps in decapod crustaceans. The numerous colleagues, who over the years have donated material to the OUMNH collections, made this study possible, and are gratefully acknowledged. Tin-Yam Chan (National Taiwanese Ocean University) is thanked for allowing us to sequence the material of *N. tenuipes*. Arlene Wheatley is thanked for her help in the lab. Two anonymous reviewers are thanked for their constructive comments on the manuscript. The work of the first author was partially supported by Thomson Unicmarine Ltd.

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### **Chapter 3: Morphometrics of *Palaemon***

A geometric morphometric analysis of two reported morphological forms of  
*Palaemon longirostris* along European Atlantic coasts.



**A geometric morphometric analysis of two reported morphological forms of  
*Palaemon longirostris* along European Atlantic coasts**

**Abstract**

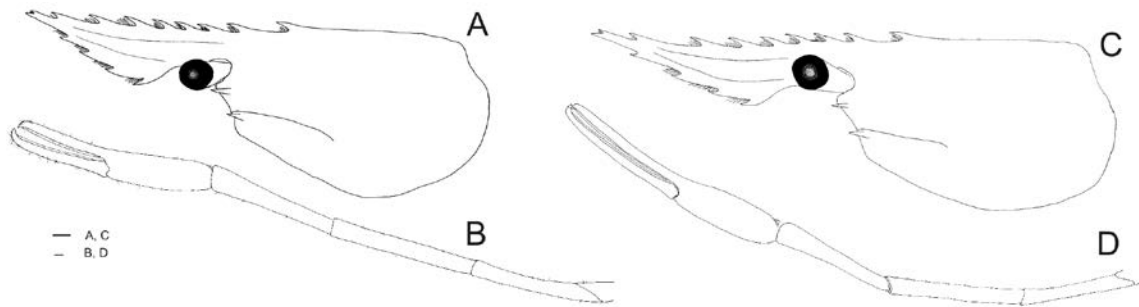
The structure of the carapace and rostrum of the estuarine shrimp *Palaemon longirostris* throughout its geographic range were investigated using geometric morphometric methods. *Palaemon longirostris* occurs in estuaries along European Atlantic coasts and previous studies have indicated inherent variability in the morphology of the species. The results of this study indicate the occurrence of two morphological forms in the region with a northern morph occurring from the Netherlands southwards to the Bay of Biscay and a southern morph occurring along the western and southern coast of the Iberian Peninsula. These forms do not appear to have any biological grounding in either historical or current evolutionary drivers and further work is suggested to elucidate the status of these morphs.

**Introduction**

The shrimp *Palaemon longirostris* H. Milne Edwards, 1837 was described from near Bordeaux in the Garonne Estuary, France and occupies a large geographic range in north-west Europe extending from south-east Britain and Germany southwards to southern Spain and to the Atlantic Coast of Morocco (d'Udekem d'Acoz, 1999). Its occurrence in the Mediterranean, particularly a recent record from a marine cave in Italy (Denitto et al., 2009), requires confirmation (d'Udekem d'Acoz, 1999), as does a recent record from the Black Sea (Sezgin et al., 2007). It is typically found in estuaries, brackish waters and reduced salinity water and is commercially exploited in many parts of its range (Holthuis, 1980).

Records attributed to *P. longirostris* show a high degree of morphological variability in the shape and robustness of the pereopods and the cephalothorax trending towards more slender and elongate pereopods, chelae and rostra in southern populations (Figure 1). This has led to northern and southern populations being variously regarded as morphological varieties of a single species (De Man, 1915, 1923; González-Ortegón & Cuesta, 2006) or as distinct species (Holthuis, 1950; Zariquiey Álvarez, 1968), and resulting in a long and complex nomenclatorial history.

The decision to recognise *P. garcicidi* Zariquiey Álvarez, 1968 as a valid species has been contentious (Lagardère, 1971) and the most recent work on *Palaemon* in northern Europe (González-Ortegón & Cuesta, 2006) concluded that there is a single species with a northern and southern morph with the divide between these two morphs occurring in the south of the Bay of Biscay. However, this rather nebulous concept of two ‘morphs’ has not been subject to any rigorous examination.



**Figure 1.** *Palaemon longirostris* H. Milne Edwards, 1837. A, cephalothorax, northern female; B, right pereopod 2 from same; C, cephalothorax, southern female; B, right pereopod 2 from same. A, B, specimen from the Thames Estuary, specimen not accessioned; C, D, specimen from the Guadalquivir estuary, specimen not accessioned. All scale bars indicate 1.0 mm.

Standard morphometric techniques have long been used in the study of crustaceans to investigate regional or inter-specific differences. These traditional morphometric techniques deal with absolute characters, for example things that can be measured or quantified; such techniques have been extensively used in the study of shrimps (e.g. De Man, 1915; Anger & Moreira, 1998; De Grave & Diaz, 2001; Mariappan & Balasundarum, 2004; García-Dávila et al., 2005; Campos et al., 2009). However, as the various synonyms of *P. longirostris* have been described based primarily on subjective differences in shape rather than quantitative or absolute characters, traditional morphometric techniques are inadequate to quantify variation in this species. In palaemonid shrimps changes in shape may be indicative of either inter-specific variation or intra-specific variation caused by ecology, maturity, social dominance or sexual dimorphism. Analysis of variation in shape is therefore desirable and should enable more objective decisions to be made on the described morphs of *P. longirostris*. The recent advent and application of landmark based geometric morphometric methods to quantify differences in shape provides the



opportunity to examine the shape variation of *P. longirostris* in a new light. Geometric morphometric methods provide fresh opportunities to biologists and taxonomists working on taxonomically problematic groups, particularly those where few definitive or meristic characters occur, as they allow the quantification of changes in shape and the statistical examination of their role in discriminating species or populations of the same species. With their semi rigid exoskeletons, crustaceans make ideal candidates for the application of geometric morphometrics (Rufino et al., 2006). Indeed, these methods have recently been successfully applied in the study of various crustaceans to document variation between (e.g. Hiller et al., 2006; Riedlecker et al., 2009) and within (e.g. Rosenberg, 2002; Rufino et al., 2006; Giri & Loy, 2008; Silva et al., 2010; Trevisan et al., 2012; Hepp et al., 2012; Lezcano et al., 2012; Zimmermann et al., 2012) species.

In this study we apply landmark based geometric morphometric analyses to the carapace and rostrum of *Palaemon longirostris* from across its geographic range to examine the degree of variation in these structures to investigate the described morphological forms.

## **Material and Methods**

### *Image Capture and Specimen Selection*

Specimens were sourced from either museum collections or were freshly collected. Adams et al., (2004) have cited the inability to account for missing areas of biological form as a limitation of geometric morphometric methods and so specimens with obvious signs of damage, deformation or regeneration were discounted from the analysis. Three hundred and fifty-six specimens were included in the study. A list of examined specimens and their provenance is provided in Table 1.

All specimens were photographed using a Leica DFC 420 camera mounted on a Leica MZ 95 microscope and using the Leica Application Suite software. All captured images were of the left side of the carapace. Geometric morphometric methods can be sensitive to image quality and differences between images captured using different methods have been reported (Rufino et al., 2006). For this reason all images were captured by a single individual using the same equipment at the same magnification. This had the disadvantage that some specimens (n = 4) that were too

large to be photographed under the microscope had to be discounted from the analysis.

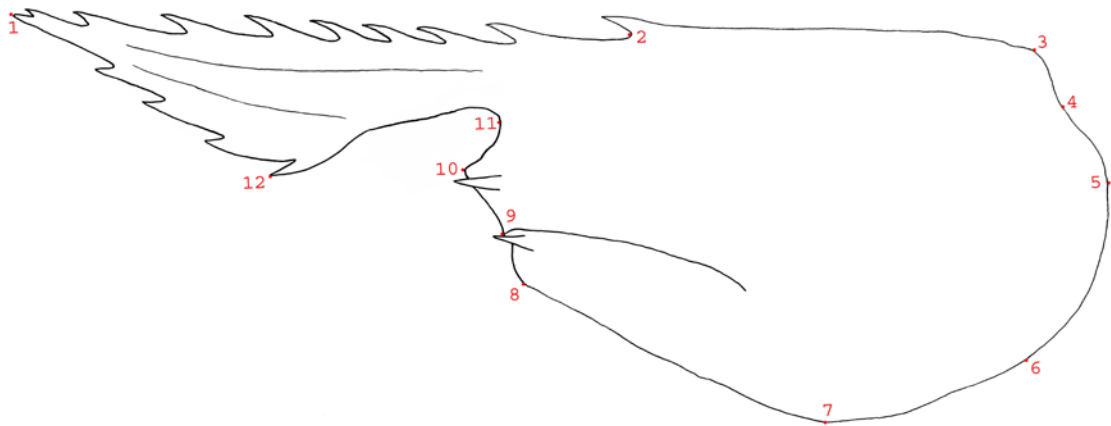
All examined specimens were sexed and measured. Post orbital carapace length (pocl., +/- 0.1 mm) was used as the standard measurement of size and measurements were made using an optical micrometer fitted to the eyepiece of a Nikon SMZ-U stereo microscope. The presence (males) or absence (females) of an appendix masculina on the second pleopod was used to determine gender in most cases but in individuals that were lacking their second pleopods the position of the gonopods was used. More males (n = 209) than females (n = 147) were available for analysis.

**Table 1.** Specimens of *Palaemon longirostris* examined in this study. Institutional abbreviations used are: NHM (Natural History Museum, London), OUMNH.ZC (Oxford University Museum of Natural History Zoological Collection).

Country	Location	Males	Females	Total	Accession Number
Belgium	Schelde Estuary	26	19	45	OUMNH.ZC 2006-31-0002
England	Thames Estuary	55	12	67	OUMNH.ZC 2012-01-0070
France	Gironde Estuary	72	4	76	OUMNH.ZC 2012-01-0073
France	Gironde Estuary	3	6	9	OUMNH.ZC 2008-01-0012
France	Gironde Estuary	6	5	11	OUMNH.ZC 2008-01-0004
France	Gironde Estuary	1	1	2	OUMNH.ZC 2007-10-0001
France	Adur Estuary	5	13	18	OUMNH.ZC 2008-01-0011
France	Loire Estuary	3	14	17	OUMNH.ZC 2008-01-0009
France	Seine Estuary	12	17	29	OUMNH.ZC 2008-01-0010
Portugal	Tagus	4	9	13	OUMNH.ZC 2012-01-0071
Portugal	Guadiana Estuary	10	3	13	-
Portugal	Mira Estuary	12	16	28	NHM 1986.260
Spain	Guadalquivir Estuary	0	4	4	OUMNH.ZC 2012-01-0073
Spain	Guadalquivir Estuary	0	6	6	NHM 1911.11.8.2038-2042
Spain	Guadalquivir Estuary	0	7	7	OUMNH.ZC 2012-06-0007
Spain	Guadalquivir Estuary	15	3	18	OUMNH.ZC 2005-03-0001

*Landmark definition and digitisation*

Twelve landmarks were selected on the carapace (Figure 2). These landmarks were selected for relative ease of identification, to provide sufficient information on the entire shape of the carapace, and their apparent homology. Where possible, landmarks were located at specific locations (Type 1 Landmarks) as these are considered optimal (Bookstein, 1991: LM 1, 2, 9 and 12) but curvature minima and maxima landmarks (Type 2 Landmarks) were used in the majority of cases (all other landmarks). Landmarks were acquired and digitised using the *tpsDig* v. 2.16 program (Rohlf, 2010).



**Figure 2.** Position of the 12 landmarks used in this study.

*Statistical analyses*

Geometric morphometric analyses were conducted using *MorphoJ* v. 1.05b (Klingenberg, 2011). ANOVA was conducted using SPSS and R v. 2.13.0 (R Development Core Team, 2011) was used to conduct the MANOVA.

Specimens were a-priori grouped to reflect the supposed division in form reported by González-Ortegón & Cuesta (2006). Thus specimens from Portugal and Spain were treated as southern and those from the Bay of Biscay and northwards were regarded as northern. Details of the specimens included in each region are presented in Tables 1 and 2.

**Table 2.** Number of specimens in northern and southern regions included in the analysis.

	Northern	Southern	Total
Male	211	45	256
Female	41	59	100
Total	252	104	

For each region a generalised least-squares Procrustes superimposition was used to remove non-shape variation (effects of rotation, translation and the isometric effects of size). This process comprises three steps. 1) raw landmark coordinates of each configuration are divided by the corresponding centroid size (i.e. the square root of the sum of the squared distances from each landmark to the centroid of the configuration) to scale all configurations to a common size; 2) the configurations are translated so that their centre of gravity matches; 3) the configurations are rotated to minimise the distance among corresponding landmarks (Zelditch et al., 2004; Zimmermann et al., 2012). PC scores were used as shape variables in all subsequent shape analyses. Log of the centroid size was used as a size variable.

This approach was used largely for congruence with other studies (e.g. that of Zimmermann et al., 2012) but also as it provides a robust framework for the analysis of data. ANOVA tests for the differences in shape between groups, giving the among group variance, the within group variance, the total variance, the statistical significance of the difference and the percentage of variance explained by the group difference. This test is widely used to assess the relative magnitudes of measurement error from repeat measurements (Klingenberg et al., 2002). MANOVA was used as an appropriate technique to test the association between shape and other variables, in this case with sex and population (northern or southern).

#### *Analysis of size*

A nested ANOVA on log centroid size was conducted to investigate variation in carapace size between estuaries. Estuaries were included as a nominal variable

nested into region (northern/southern). Multiple pairwise t-tests were run to detect statistically significant differences among estuaries.

#### *Analysis of shape*

Shape data were examined using a principal component analysis (PCA) applied to the Procrustes coordinates. To test whether individuals from northern and southern regions differ morphologically from one another a MANOVA was applied to the PC scores. In order to visualise the relationship among groups, canonical variate analyses (CVA) were performed using northern and southern as classifying parameters with the permutation test for pairwise distances set to 10000 iterations.

### **Results**

#### *Differences in size*

Statistically significant differences in size were obtained between morph (northern or southern) ( $p = 0.001$ ) and sex ( $p = <0.001$ ) (Table 3). Southern females are the largest, slightly larger than northern females. Southern males are smallest with a large difference detected between southern and northern males (Figure 3).

#### *Differences in shape*

Statistically significant differences in shape were observed between northern and southern morphs (Table 3) which are illustrated in Figure 4. Two morphological groups are distinguished according to PC1 (Figure 4). The first group have mostly negative PC1 values, whilst the second group have mostly positive PC1 values corresponding to southern and northern populations respectively. The canonical variate plots, where region and sex have been used as grouping factors (Figures 4 and 5), confirm this observation with separation of northern and southern morphs in both males and females.

Shape reconstructions were produced using a multivariate regression. The difference in shape primarily relates to the shape and length of the rostrum (Figure 7). The analysis of the residuals of the multivariate regression of the shape variables

demonstrates statistically significant differences between northern and southern morphs (Table 3).

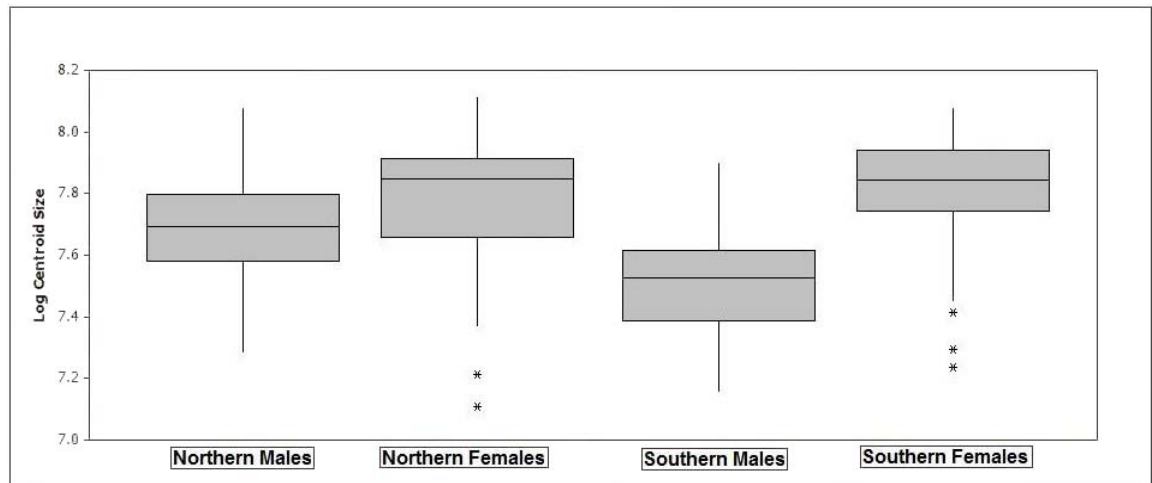
**Table 3.** Effect of morph (northern or southern) and sex on log centroid size (ANOVA) and on shape (MANOVA).

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>P-value</b>
Corrected Model	3	2.656 <sup>a</sup>	0.885	29.812	<0.001
Sex	1	2.513	2.513	84.646	<0.001
Morph	1	0.353	0.353	11.895	0.001
Sex * morph	1	0.744	0.744	25.047	<0.001
Error	352	10.452	0.030		
Corrected Total	355	13.108			

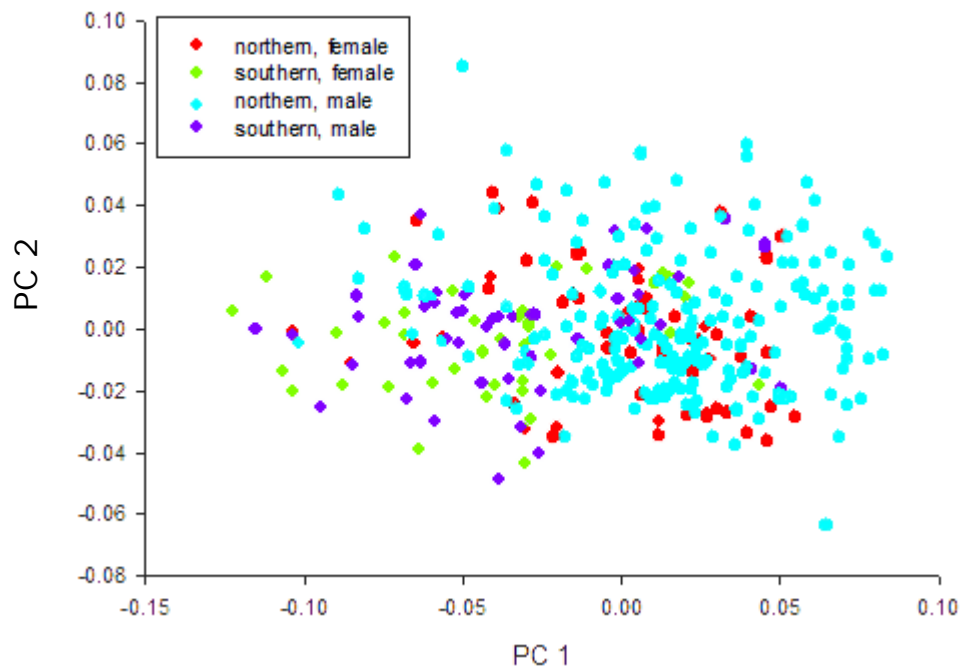
  

	<b>df</b>	<b>Pillai</b>	<b>Approx. F</b>	<b>Numerator df</b>	<b>Denominator df</b>	<b>P-value</b>
Sex	1	0.24446	5.3871	20	333	<0.001
Morph	1	0.34565	8.7950	20	333	<0.001
Sex * morph	1	0.03744	0.6476	20	333	0.1
Residuals	352					

<sup>a</sup> R Squared = 0.203 (Adjusted R Squared = 0.196); SS, Type III Sum of Squares; df, degrees of freedom; MS, mean squares.



**Figure 3.** Log of the mean centroid size for northern and southern populations for males and females



**Figure 4.** PCA plot for shape configurations projected onto the first two principal components.

**Table 4.** PCA covariance matrix based on Procrustes coordinates, pooled by sex and population.

	Eigenvalues	% Variance	Cumulative %
1.	0.00104238	40.864	40.864
2.	0.00042823	16.788	57.651
3.	0.00025290	9.914	67.566
4.	0.00016348	6.409	73.974
5.	0.00013825	5.420	79.394
6.	0.00010546	4.134	83.529
7.	0.00008912	3.494	87.022
8.	0.00006580	2.580	89.602
9.	0.00005521	2.164	91.766
10.	0.00004370	1.713	93.479
11.	0.00003415	1.339	94.818
12.	0.00003125	1.225	96.043
13.	0.00002115	0.829	96.872
14.	0.00001954	0.766	97.639
15.	0.00001676	0.657	98.296
16.	0.00001257	0.493	98.788
17.	0.00001025	0.402	99.190
18.	0.00000882	0.346	99.536
19.	0.00000742	0.291	99.827
20.	0.00000442	0.173	100.000

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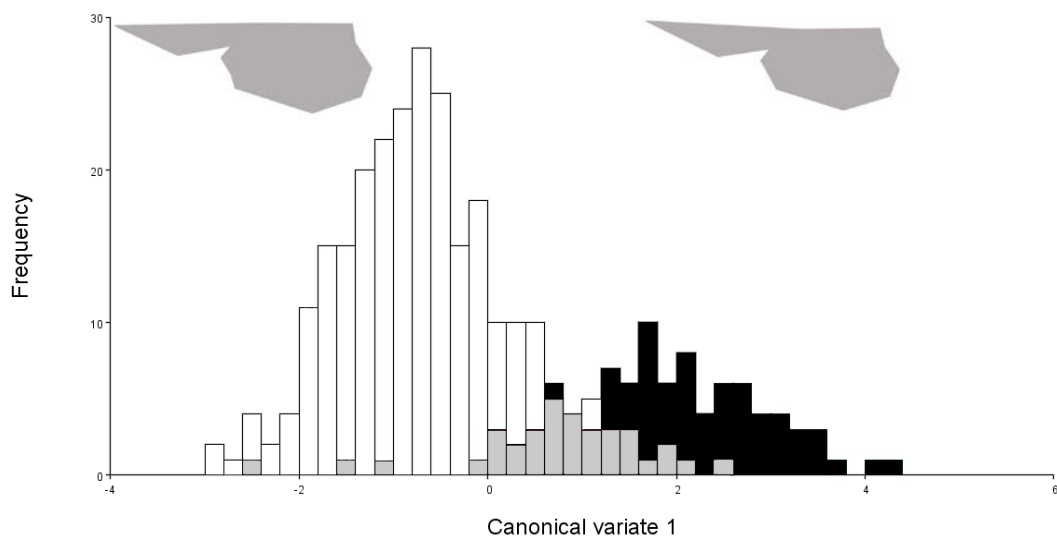
Total variance: 0.00255087



## Discussion

In this study, the morphology of the carapace and rostrum of *Palaemon longirostris* has been investigated using geometric morphometric methods. These techniques have found wide application in the biological sciences (Richtsmeier et al., 2002) and are being increasingly used to quantify organisms' shape (Riedlecker et al., 2009). Cruz et al. (2012) highlighted the usefulness of geometric morphometrics in assessing variations in form, particularly for taxa whose systematics has proved challenging or whose nomenclature has long been debated. Geometric morphometrics are also regarded as more useful in discrimination amongst populations than traditional morphometrics (Maderbacher et al., 2008).

The results of this study support the contention of a northern and southern morph of *Palaemon longirostris* with a divide between the two morphs between the south of the Bay of Biscay and the west coast of the Iberian Peninsula, in keeping with the assertion of González-Ortegón & Cuesta (2006).



**Figure 5.** Female (above) and male (below) CVA plots using region as a grouping factor with shape reconstructions for each region. Black = southern, white = northern.

The southern and northern morphs differ chiefly in the length and direction of the rostrum, with the southern morph exhibiting a longer and more upturned rostrum (Figure 7). Variation in both the form and dentition of the rostrum has been described

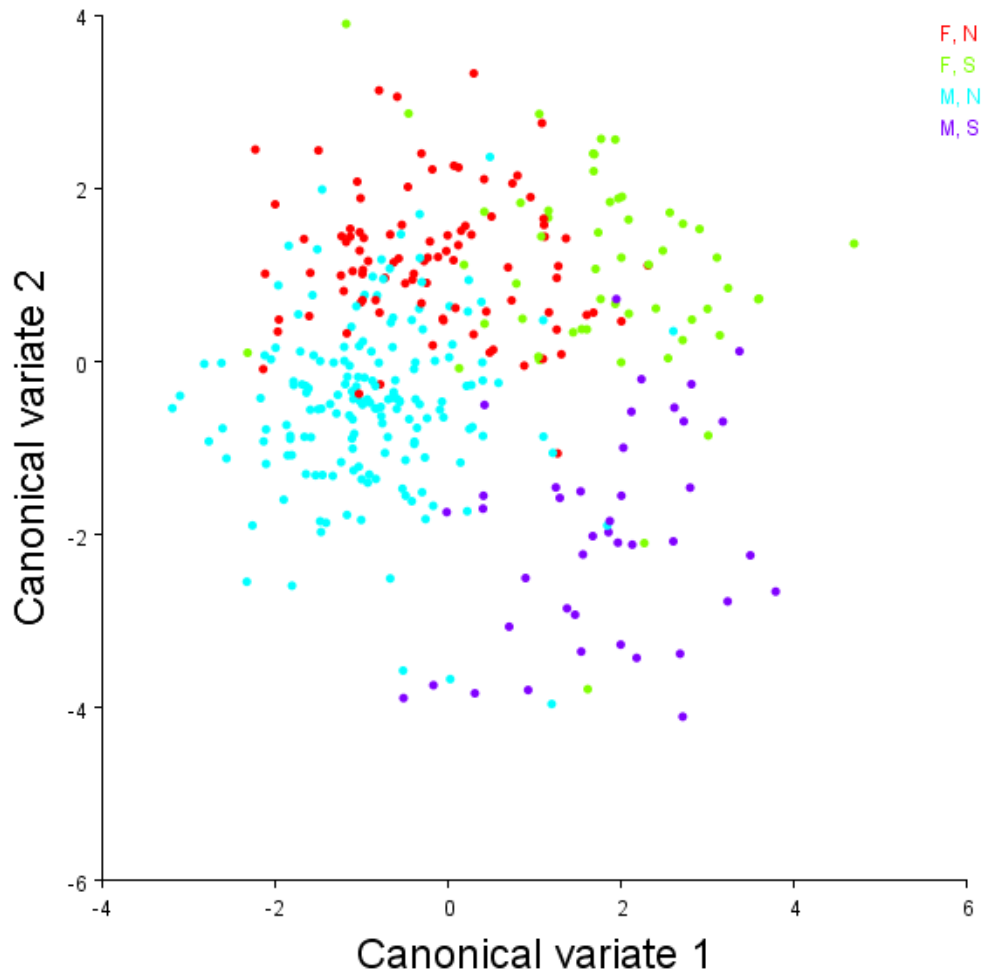
in a range of caridean species at the population (e.g. De Grave, 1999a, b), habitat (e.g. Zimmermann et al., 2012), local (e.g. Yaldwyn, 1957; De Grave, 1999a; Covich et al., 2009; Jugovic et al., 2010) and regional levels (e.g. De Grave, 1999a; Anastasiadou et al., 2004).

Changes in morphology are normally driven by either environmental or genetic factors (De Grave & Diaz, 2001; Remerie et al., 2005) or a combination of these, and the driving factors behind morphological changes may vary according to temporal and geographic scale. González-Ortegón & Cuesta (2006) cite unpublished genetic evidence to support the contention that *P. longirostris* represents a single species throughout its range. Furthermore, comparison of the 16SrRNA sequence retrieved by Ashelby et al. (2012) for a specimen from the Thames, that presented by Cuesta et al. (2012) for a specimen from the Guadalquivir and others from GenBank (Cartaxana, unpubl.) revealed no significant genetic differences (T. Page, pers. comm.). COI sequences from Cartaxana (unpubl.) also revealed no significant differences (T. Page, pers. comm.) but the northern population is currently only represented on GenBank by a single sequence. However, this suggests that the populations are not reproductively isolated and that contemporary gene flow occurs. The occurrence of two morphs witnessed in the present study therefore is more likely to result from an environmental influence or historic process on the expression of form.

Possible environmental factors that may have an influence on morphology include temperature, salinity, food availability, water flow or competitive or predator/prey interactions (Remerie et al., 2005).

Recently, Zimmermann et al. (2012) demonstrated significant differences in the form of the carapace and shape of the rostrum of *Macrobrachium australe* in relation to habitat. Their study found that specimens of *M. australe* from populations from lotic habitats had a shorter, more robust and straighter rostrum than those from lentic environments. Similarly, Giri and Loy (2008) demonstrate differences in rostral length and the robustness of the carapace between lake and river populations in two species of the freshwater anomuran genus *Aegla*. Both Zimmermann et al. (2012) and Giri and Loy (2008) consider the possibility that other factors that co-vary with current speed may contribute to the documented variation. Such hydromorphological characteristics were considered by Nicolas et al. (2010) who classified 135 European estuaries into seven broad groupings. Whilst the southern morph of *P. longirostris*

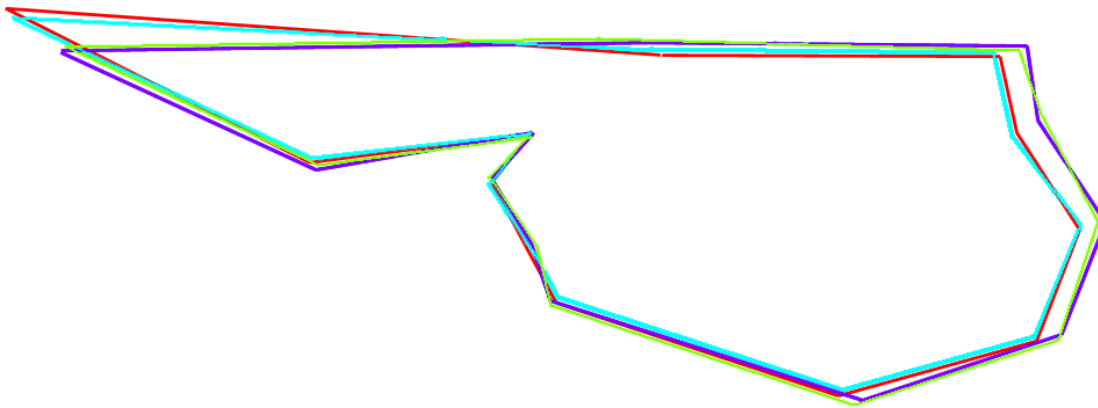
only inhabits Nicolas et al.'s (2010) Type A estuaries the northern morph inhabits both Type A and Type B. These two estuarine types are chiefly distinguished through latitude, continental shelf width and source elevation. The occurrence of the northern morph of *P. longirostris* in both types of estuary suggests that these factors do not influence its morphology.



**Figure 6.** Scatter plot of canonical variate 1 (region) against canonical variate 2 (sex).

The ecological and habitat requirements of *P. longirostris* are similar throughout its range (e.g. Marchand & Alliot, 1981; Sorbe, 1983; Van den Brink & Van der Velde, 1986, Cartaxana, 1994; Attrill & Thomas, 1996; González-Ortegón et al., 2006) and therefore the potential effects of many environmental variables can be

discounted as influential factors on rostral morphology. A gradual increase in summer maxima and winter minima temperatures does occur from the north to the south of its range. *Palaemon longirostris* currently inhabits temperatures that range between 5 and 20°C in the Thames (Attrill & Thomas, 1996), 2 and 26°C in the Gironde Estuary (Lobry et al., 2006), and between 11 and 28°C in the Guadalquivir (González-Ortegón et al., 2006). However, these contemporary temperature differentials are relatively small and it is difficult to see how they would affect the form of the rostrum in a population.



**Figure 7.** Comparison of the shape of southern and northern morphs of *Palaemon longirostris*. Red line – northern female, turquoise line – northern male, green line – southern female, purple line – southern male. Images aligned on landmark 11.

A further explanation is that the differences in morphology have a historical grounding. During the last ice age (27-15 ka BP) much of Northern Europe was covered by the ice sheet reaching its southern limit just south of the Baltic Sea and central Britain to about 53°N. Permafrost was present as far south central France to just south of the Gironde to about 44°N. Sea ice covered much of the Bay of Biscay to the northern Iberian Peninsula (See Figure 1B in Hewitt, 1999 for distribution of these features). The western and southern Iberian Peninsula were largely ice free and are considered one of the refugia from the Pleistocene ice age (Ben-Schlomo et al., 2006; Remerie et al., 2009). Other refugia are believed to have existed in the English Channel around Brittany (Ben-Schlomo et al., 2006; Remerie et al., 2009). A hypothesis suggested here for the two morphological forms of *P. longirostris* is that

populations of the species presented a continuous distribution in suitable habitats along European Atlantic coasts prior to the glaciation. During the ice age the population became fragmented with pockets surviving in refugia in the region of the English Channel as well as the Iberian Peninsula. These isolated pockets developed according to the main environmental and biotic factors present in each region. These would likely have differed between each region but may have included prey availability, predation pressure, water flows or temperature. Following retreat of the glacier the estuaries of the Bay of Biscay and northwards were recolonised from this northern refuge rather than from the south. However, such allopatric divergence should be reflected by genetic differences as demonstrated, for example, by Remerie et al. (2009) in mysids and by Gysels et al. (2004) in sand gobies. As 16SrRNA is a reasonably conserved gene, suitable for showing interspecific but not intraspecific differences, the 16SrRNA analysis of *P. longirostris* sequences quoted above would not show haplotype differences as demonstrated by the Remerie et al. (2009) and Gysels et al. (2004) studies. Analysis of COI sequences or faster evolving markers such as microsatellites from a greater number of specimens from both northern and southern populations may reveal a distinction between the populations that is not evident by the 16SrRNA analysis.

A more recent phenomenon that has been shown to profoundly affect the carapace and rostrum form of *Palaemon longirostris* is pollution. Béguer et al. (2008, 2010) report a heavy incidence of skeletal deformities occurring in the population of the Gironde Estuary since at least 1992. They report that up to 40% of the population may be afflicted by morphological abnormalities manifested in hypertrophied scaphocerites and uropods, twisted fingers of the chelae of the second pereopods, a dorsally humped carapace and down-turned rostra. Such deformities were also witnessed at lower intensity in other estuaries. Although Béguer et al. (2008) considered the possibility that micro-organism infections were causing the deformities, organic, heavy metal or radionucleotide pollutants or, more likely, cocktails of these pollutants acting in synergy (Béguer et al., 2010) were also suggested. Larger individuals were more prone to deformity than smaller specimens suggesting bioaccumulation is a factor; however, larvae with deformities can be born to apparently unaffected adults (Fueillassier et al., 2012). In the samples analysed from the Gironde in this study many specimens were discounted from the analysis due to obvious deformation so as not to bias the data. However, the extent and nature of

these deformations from the average shape could be a worthy subject of a future geometric morphometric study.

This study has applied geometric morphometric techniques to the study of two reported morphological forms of *Palaemon longirostris*. The results indicate that the form of the rostrum, which has historically been used as a contributing diagnostic character in the taxonomy of *Palaemon* species, is in fact a variable character. Several previous works have commented on the variability in the dentition of the rostrum in *Palaemon* (e.g. De Man, 1915; Kubo, 1942; Holthuis, 1950; Chace & Bruce, 1993; De Grave, 1999b) and the dentition of the rostrum has been deemphasised as a diagnostic feature as a result. The shape of the rostrum has been less well studied and the present study suggests that caution should also be advised in the emphasis placed on this feature in taxonomic descriptions. However, the variation demonstrated in the present study is not easily explained in historical or contemporary terms. For many ecological parameters *P. longirostris* displays similar or identical requirements throughout its range thus negating any potential effect. Moreover, historical processes, such as divergence during glacial maxima are not genetically supported. We cannot therefore rule out that the observed differences, whilst statistically supported, have no biological grounding. In this case the differences may be attributed to an imbalance in the design of the study or perhaps the selected landmarks.

Several aspects of the design of the study may have influenced the apparent detection of two morphological forms. The statistically significant results could in fact reflect northern/southern imbalance in specimen numbers, the bias towards northern males or a reasonably small overall sample size. No specimens from estuaries along the Cantabrian Coast were available for analysis but as the presumed divide in form is in this region it may be expected that intermediate forms may occur in this region.

In shape analysis a large change may be attributable to the effects of one or a few landmarks, commonly known as the Pinocchio effect (Zelditch et al., 2004). One of the key advantages offered by geometric morphometrics is the fact that the saved digital image can be revisited so that any shapes or landmarks that had not been previously considered can be included in the analysis (Riedlecker et al., 2009). Conversely, landmarks no longer considered valid or necessary can be excluded. By

selecting additional or alternative landmarks and reanalysing the data the potential of a Pinocchio effect could be analysed.

Due to the contradictory data obtained (genetic vs. shape) further work is necessary to determine whether there truly is a north/south divide in the morphology of *Palaemon longirostris*. This should include analysis of a greater number of specimens from a greater number of locations, the selection of alternative or additional landmarks and possibly the analysis of other structures such as pereopods, chelae or scaphocerites backed up by further genetic analysis using more quickly evolving markers. However, the recent, prevalent effects of environmental pollution reported by Béguer et al. (2008, 2010) could confound such a study.

### Acknowledgements

Paul Clark and Miranda Lowe (NHM) are thanked for the loan of specimens from their collections to facilitate this study. Michel Girardin provided specimens from the Gironde and Christoph Lejeune provided specimens from the Guadalquivir, Tagus and Guadiana estuaries for analysis. Thomson Unicmarine partially supported the work of the first author.

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## **Chapter 4: Functional morphology of *Palaemon***

Preliminary observations on the mandibles of Palaemonoid shrimp (Crustacea:  
Decapoda: Caridea).





**Preliminary observations on the mandibles of Palaemonoid shrimp (Crustacea:  
Decapoda: Caridea)**

**Abstract**

The mandible of caridean shrimps has been widely studied in the taxonomy and functional biology of the group and within the Palaemonoidea reaches a high level of structural diversity reflecting the diverse lifestyles of this superfamily. This study investigates the mandible of nine species belonging to six of the recognised families of the Palaemonoidea and analyses the results in a phylogenetic and dietary framework. The results of the study indicate that little phylogenetic information is conveyed by the structure of the mandible but that its form is influenced by primary food sources of each species. With the exception of *Anchistioides antiguensis*, all species examined possessed cuticular structures at the distal end of the *pars molaris*, which whilst superficially observed in previous studies, have not been analysed in detail to date. Five types of cuticular structures are recognised herein, each with a unique form and variable in number, placement and arrangement. Each type is presumed to have a different function which is likewise related to diet.

**Introduction**

Decapod crustaceans display a wide variety of modified mouthparts that serve both mechanical and sensory functions and have attracted the attention of taxonomists, systematicists and functional biologists for many years (e.g. Borradaile, 1917; Fujino & Miyake, 1968; Roberts, 1968; Caine, 1975; Coombs & Allen, 1978; Schembri, 1982; Felgenhauer & Abele, 1985; Garm & Høeg, 2001; Garm et al., 2003; Garm, 2004). The semi-rigid, robust mandible has been attributed a mechanical function in the breaking down of food prior to ingestion but a recent study on the mandible of larval *Palaemon elegans* demonstrated that it possesses a variety of sensillia (Geiselbrecht & Melzer, in press), suggesting that it may be a much more complex organ than a superficial study would suggest. Indeed, Borradaile (1917) in his pioneering work on the structure and function of the mouthparts of palaemonid prawns concluded that “the mandible of the Crustacea is an exceedingly complicated, varied and interesting organ, presenting many problems and worthy of a great deal

more attention than it has received”. Nearly a century on and the mandible, although superficially described in numerous taxonomic descriptions, remains understudied and very few studies have focussed on the detailed structure and potential evolutionary drivers in relation to the form of the mandible. Recent works have added to our knowledge of the mandible across a range of crustaceans but largely focus larvae (e.g. Heral & Saudray, 1979; Casanova et al., 2002; Tziouveli et al., 2011; Geiselbrecht & Melzer, in press) or are restricted to a single or a small number of species of a single genus or family (e.g. Fujino & Miyake, 1968; Caine, 1975; Coombs & Allen, 1978; Mielke, 1984; Felgenhauer & Abele, 1985; Hobbs, 1991; Moore et al., 1993; Richter, 2004; Arndt et al., 2005; Mekhanikova, 2010). Within the Palaemonoidea, the two most extensive studies on mandibles both focus on the genus *Palaemon*, using light microscopy to examine the structure and function (Borradaile, 1917 – as *Leander*) and interspecific variation (Fujino & Miyake, 1968) of this feature.

Within the infraorder Caridea, the mandible is variously developed (Burukovsky, 1986) but is frequently comprised of a *pars incisivus* (incisor process) and *pars molaris* (molar process) and may be provided with a palp or not. Both the *pars incisivus* and the *pars molaris* are variable in form ranging from truncated to elongate, straight to markedly curved, narrow to flared, widely separated to barely separated and all gradations in between (Burukovsky, 1986). The distal portions of both processes are often provided with acute or rounded lobes (‘teeth’) or ridges but may be flattened. Either the *pars incisivus* or the *pars molaris* may be reduced or absent or they may be fused together. Due to this diversity in the development and form, features of the mandible have been used in the taxonomy of caridean shrimps, particularly in families where few characters exist to differentiate genera and species. Additionally, several recent classifications of the Caridea have, in part, also been underpinned by features of the mandible (Thompson, 1967; Christofferson, 1990; Chace, 1992).

In many decapods mastication largely occurs mainly in the gastric mill (Caine, 1975). Patwardhan (1934) expressed an opinion that many carideans lack a complex gastric mill and thus the mouthparts are correspondingly more developed, although more recent studies (Felgenhauer & Abele, 1983) demonstrate their presence in a number of caridean families. Nevertheless, the mandible is involved in initial breaking down of food and therefore not only has a taxonomic significance but

obviously has a large functional significance also and thus its form may provide insights into the diet or feeding mode of the species. Species that have particular dietary regimes or feeding mechanisms tend to have correspondingly specialised mouthparts (Caine, 1975). During feeding the *pars incisivus* is believed to be mostly used in cutting and slicing of food particles into more manageable portions whilst the *pars molaris* is usually thought to have a grinding function (Bauer, 2004), although Felgenhaur and Abele (1985) found that the mandible of atyid prawns, that do possess a gastric mill, was not used for crushing food.

Whilst previous studies on shrimps have investigated mouthpart morphology of a single genus or species (Borradaile, 1917; Fujino & Miyake, 1968) or between genera belonging to the same family (Felgenhaur & Abele, 1985) only the study of Storch et al. (2001) on three Antarctic shrimps has investigated differences between families. The present study was conceived to investigate the structure of the mandible in 9 species belonging 9 genera and 6 families from the superfamily Palaemonoidea covering a diversity of form and ecology, to evaluate the hypotheses that 1) the mandible has phylogenetic significance within the superfamily and 2) its' structure is influenced by diet.

### **Material and Methods**

Eight families are currently included in the Palaemonoidea with the Palaemonidae further split into two subfamilies: the Palaemoninae and the Pontoniinae (De Grave & Fransen, 2011). However, the family Kakaducarididae is shortly to be synonymised with the Palaemonidae (Short et al., in press) leaving seven valid families. Three of these families are monogeneric (Anchistioididae, Desmocarididae and Typhlocarididae) whilst the highest diversity of both morphology and lifestyle is found in the subfamily Pontoniinae. No members of the Typhlocarididae were available for destructive examination via SEM and references to the morphology of the mandible in *Typhlocaris* are based on descriptions in the literature (Calman, 1909; Parisi, 1921; Caroli, 1923; 1924; Tsumamal, 2008). Despite several attempts to process left mandibles of *Euryrhynchus*, none survived the sonication stage intact and therefore observations are based on the right mandible only. All specimens studied are held in the Zoological Collection of the Oxford

University Museum of Natural History (OUMNH.ZC) with details included in Table 1.

**Table 1:** Species and provenance of specimens examined via SEM in this study.

<b>Species</b>	<b>Accession Number</b>
<b>Family Palaemonidae</b>	
<b>Subfamily Palaemoninae</b>	
<i>Palaemon macrodactylus</i> Rathbun, 1902	OUMNH.ZC 2006-01-0039
<i>Macrobrachium nipponense</i> (De Haan, 1849)	OUMNH.ZC 2012-01-0060
<b>Subfamily Pontoniinae</b>	
<i>Pontonia pinnophylax</i> (Otto, 1821)	OUMNH.ZC 2008-11-0081
<i>Periclimenaeus caraibicus</i> Holthuis, 1951	OUMNH.ZC 2009-01-0101
<b>Gnathophyllidae</b>	
<i>Gnathophyllum elegans</i> (Risso, 1816)	OUMNH.ZC 2011-09-0005
<b>Hymenoceridae</b>	
<i>Hymenocera picta</i> Dana, 1852	OUMNH.ZC 2010-04-0017
<b>Desmocarididae</b>	
<i>Desmocaridus bislineata</i> Powell, 1977	OUMNH.ZC 2009-19-0001
<b>Euryrhynchidae</b>	
<i>Euryrhynchus wrzesniowskii</i> Miers, 1877	OUMNH.ZC 2006-21-0001
<b>Anchistioididae</b>	
<i>Anchistioides antiguensis</i> (Schmitt, 1924)	OUMNH.ZC 2007-14-0001

The methods used for preparation of tissue follow those established by Martin et al. (2007) and De Grave and Goulding (2011). Mandibles were carefully dissected from specimens stored in 75% ethanol. After removal mandibles were passed through a graded ethanol series to distilled water, subjected to brief (5-15 seconds) sonication using a light surfactant, then re-hydrated in graded ethanol to 100%, with drying done via the HMDS (hexamethyldisilazane) method. Dried specimens were coated with a gold-palladium mixture in a Polaron E5000 coating unit and observed in a JEOL JSM-5510 microscope.

The naming of the teeth on the *pars molaris* refers to their position *in situ* and follows Fujino and Miyake (1968). Setal definitions follow Garm (2004).

## Results

The most common form of mandible of those species studied is bipartite, with a well developed *pars incisivus* and *pars molaris* (Table 2). The *pars incisivus* is reduced to an acute process in *Gnathophyllum elegans* (Tables 2 and 3; Figure 5A) and absent in *Hymenocera picta* (Tables 2 and 3; Figure 4D). In all other species the structure of the *pars incisivus* is similar (Table 3) being flattened and provided with teeth distally. In *Pontonia pinnophylax*, a series of denticles is also present along the posterior margin (Table 3; Figures 3A, 3C).

A mandibular palp is present only in *P. macrodactylus* (Table 2) and *M. nipponense* (Table 2; Figure 2C). In both these species the structure of the palp is similar being three segmented (but see Fujino & Miyake, 1968 for discussion on variation in this character in *P. macrodactylus*), with the distal segment being more slender and slightly longer than the basal and penultimate segments. Distally serrulate setae are present (Figure 1D) on all segments of the palp but most numerous on the distal segment.

A great diversity of form is found in the *pars molaris*. In all species examined the *pars molaris* is well developed and ranges from rounded (*Palaemon macrodactylus*, *Macrobrachium nipponense*, *Periclimenaeus caraibicus*, *H. picta*), oval (*G. elegans*, *Desmocarid bislineata*, *Euryrhynchus wrzesniowskii*), slightly squared (*P. pinnophylax*, *Anchistioides antiguensis* right) to roughly triangular (*A. antiguensis* left) in cross-section. Most are roughly parallel sided but those of *H. picta* and *G. elegans* are strongly curved, that of *D. bislineata* has convex lateral margins and in *A. antiguensis* the *pars molaris* is strongly flared distally. Teeth are present distally on most mandibles (*Palaemon*, Figures 1A, 1E; *Macrobrachium*, Figures 2A, 2C-D; *Pontonia*, Figures 3B, 3D; *Anchistioides*, Figures 7D-F; *Hymenocera*, Figures 4E-F; *Gnathophyllum*, Figure 5D), whilst in others these are fused to form lip-like structures (*Euryrhynchus*, Figures 7A-B; *Periclimenaeus*, Figures 4A-C) and in *Desmocarid* no teeth are present and the distal end is a ridged plate (Figures 6A-B, 6D-F). The form of the teeth is highly variable with spine-like teeth being present in *Hymenocera* (Figures 4E-F), a blade like tooth being present in

*Gnathophyllum* (Figure 5D) and more lobate teeth present in the other species. The lobate teeth may be reduced to low mounds or massively produced with the tips entire or bifid as well as all gradations in between. Significant differences in the arrangement and structure of the teeth are also noted between the left and right mandibles. Typically four teeth are present although in some species these are modified such that they are difficult to discern. Table 4 summarises the broad arrangements of teeth found in each species. For greater detail the reader is referred to the figures cited in that table.

In addition to the teeth and cusps mentioned above, the distal end of the *pars molaris* of most mandibles examined here were found to be covered, to a greater or lesser degree, by numerous filamentous structures, which are flexible to semi-rigid and frequently developed into rows (Figures 1B-C, 1F, 2A-B, 3E, 3F, 4B-C, 4E-F, 5A-D, 6A-F, 7A-C). The individual filaments do not conform to any described form of seta nor to the definition of a seta, as described and defined by either Watling (1989) or Garm (2004), in particular lacking a complete basal articulation and a continuous lumen. The arrangement, placement and ultra-structure of these cuticular structures (CS) is highly variable between the species included in the analysis but they can be broadly classified into five types. Type I CS are semi rigid, parallel sided or slightly tapered distally and between 40 and 60  $\mu\text{m}$  long and 3-6  $\mu\text{m}$  wide and tend to form rows. They are found in *Palaemon* (Figures 1B-C, F), *Macrobrachium* (Figures 2A-B, D), *Pontonia* (Figures 3B, D-F) and *Euryrhynchus* (Figures 7A-C). In *Euryrhynchus* shorter structures are also present (Figures 7C) but these appear structurally similar to Type I structures and are regarded as the same type. Type II CS are found only in *Periclimenaeus*. These appear more rigid and slightly stouter than Type I structures and form tufts rather than rows (Figures 4B-C). Type III CS are found in *Gnathophyllum*. They are approximately 60  $\mu\text{m}$  long and 5  $\mu\text{m}$  wide, highly flexible, taper strongly distally with a feathered inner margin and have a weak constriction basally (Figures 5A-D). They form a dense covering over the entirety of the distal end of the *pars molaris*. Type IV CS (Figures 4E-F) are very similar to Type III differing chiefly in lacking a feathered inner margin and a weak basal constriction. They are found in *Hymenocera*. Type V CS are unique to *Desmocarid* and are the most highly modified. They comprise about 12 finger-like projections arising from a basal column (Figures 6B-D, F). No cuticular structures were observed on the mandibles of *Anchistioides antiguensis*. The details of the positioning and

arrangement of the structures are presented in Table 5 and the figures referred to therein.

These cuticular structures have been noted in several previous studies or taxonomic descriptions (e.g. Borradaile, 1917; Fujino & Miyake, 1968; Felgenhauer & Abele, 1985; Storch et al., 2001; Fransen, 2006 to name but a few), where the elements have typically been referred to as setae or bristles, but no detailed study of these features has been conducted to date. In some species setules are also noted on the disto-lateral margins (Figures 4F, 6B-C, 6E-F).

**Table 2.** Summary of the features of the mandibles examined in this study. + = present, - = absent, r = reduced.

	<i>Pars molaris</i>	<i>Pars incisivus</i>	<i>Cuticular structures</i>	<i>Mandibular palp</i>
<i>Palaemon macrodactylus</i>	+	+	Type I	+
<i>Macrobrachium nipponense</i>	+	+	Type I	+
<i>Pontonia pinnophylax</i>	+	+	Type I	-
<i>Periclimenaeus caraibicus</i>	+	+	Type II	-
<i>Gnathophyllum elegans</i>	+	+/r	Type III	-
<i>Hymenocera picta</i>	+	-	Type IV	-
<i>Desmocariss bislineata</i>	+	+	Type V	-
<i>Euryrynchus wrzesniowski</i>	+	+	Type I	-
<i>Anchistioides antiguensis</i>	+	+	-	-

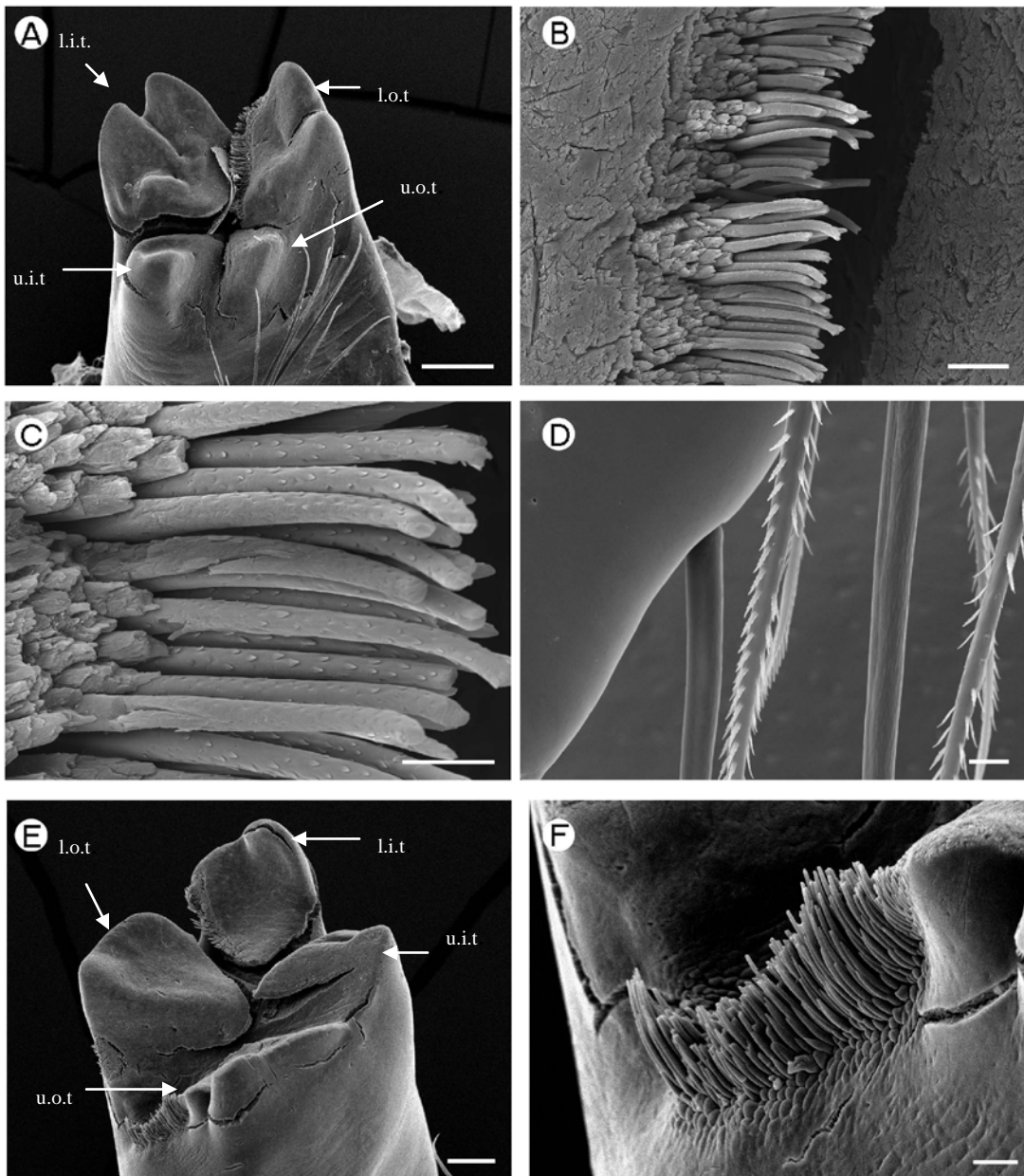
**Table 3.** Details of the *pars incisivus* of each species examined.

	Right				Left			
	Form	Anterior margin	Posterior margin	Teeth	Form	Anterior margin	Posterior margin	Teeth
<i>Palaemon macrodactylus</i>	About twice as tall as wide	Strongly convex	Straight to slightly concave	3, approximately equal, widely-spaced, triangular.	About twice as tall as wide	Strongly convex	Straight to slightly concave	4, widely-spaced, triangular, outer teeth slightly larger than inner teeth.
<i>Macrobrachium nipponense</i> Figure 2C	Height equal to width of basal portion, narrowing strongly distally	Strongly convex	Concave	2, approximately equal, widely-spaced, triangular.	Very broad, wider than long in middle portion	Strongly convex	Straight	3, very robust, triangular, anterior most tooth acute, remaining teeth with rounded tip.
<i>Pontonia pinnophylax</i> Figures 3A, 3C	Elongate, slender, equal in length to <i>pars molaris</i> , strongly curved distally.	Straight, roughly parallel with posterior	Straight, roughly parallel with anterior with seven denticles	4, triangular, outer teeth larger and broader than inner teeth.	Elongate, slender, equal in length to <i>pars molaris</i> , strongly curved distally.	Straight roughly parallel with posterior	Straight, roughly parallel with anterior with five denticles	5, triangular, acute, posterior-most the largest, remaining teeth approximately equal size.
<i>Periclimenaeus caraibicus</i>	Slender, ribbon-like, slightly twisted and slightly shorter than <i>pars molaris</i>	Straight roughly parallel with posterior	Straight roughly parallel with anterior	Distally damaged in present specimen, detail from Holthuis (1951): Small acute teeth present distally, about 10 in number.	Laminar in form, slightly curved and slightly shorter than <i>pars molaris</i> .	Convex	Concave	Distal margin broadly rounded, tapering posteriorly, armed with 11 small, acute teeth.
<i>Gnathophyllum elegans</i> Figure 5A	Reduced to an acute lobe	-	-	-	Reduced to an acute lobe	-	-	-
<i>Hymenocera picta</i>	Absent	-	-	-	Absent	-	-	-
<i>Desmocarid bislineata</i> Figure 6A	Slightly shorter than <i>pars molaris</i> , about 3.5 times as long as wide, slightly curved inwards.	Slightly convex	Slightly concave	4, approximately equal, widely-spaced, triangular	Similar to that of the right mandible, but slightly broader in median part.	Slightly convex	Slightly concave	4, approximately equal, widely-spaced, triangular
<i>Euryrhynchus wrzesniowski</i>	Elongate, slender, about 3.5 times as long as wide, parallel sided, slightly curved inwards.	Straight roughly parallel with posterior	Straight roughly parallel with anterior	4, widely-spaced, triangular, anterior-most slightly larger than remaining three.	Not Examined	-	-	-
<i>Anchistioides antiguensis</i> Figures 7D, 7F	Broad, about 3 times as long as wide, slightly twisted. Equal to, or slightly longer than <i>pars molaris</i> .	Slightly convex	Slightly concave	3, widely-spaced, triangular, acute, outer two broader and longer than median tooth.	Broad, about 3 times as long as wide, slightly twisted. Equal to, or slightly longer than <i>pars molaris</i> .	Strongly convex	Straight to slightly concave.	3, widely-spaced, triangular, acute, teeth distally, outer two broader and longer than the median tooth.

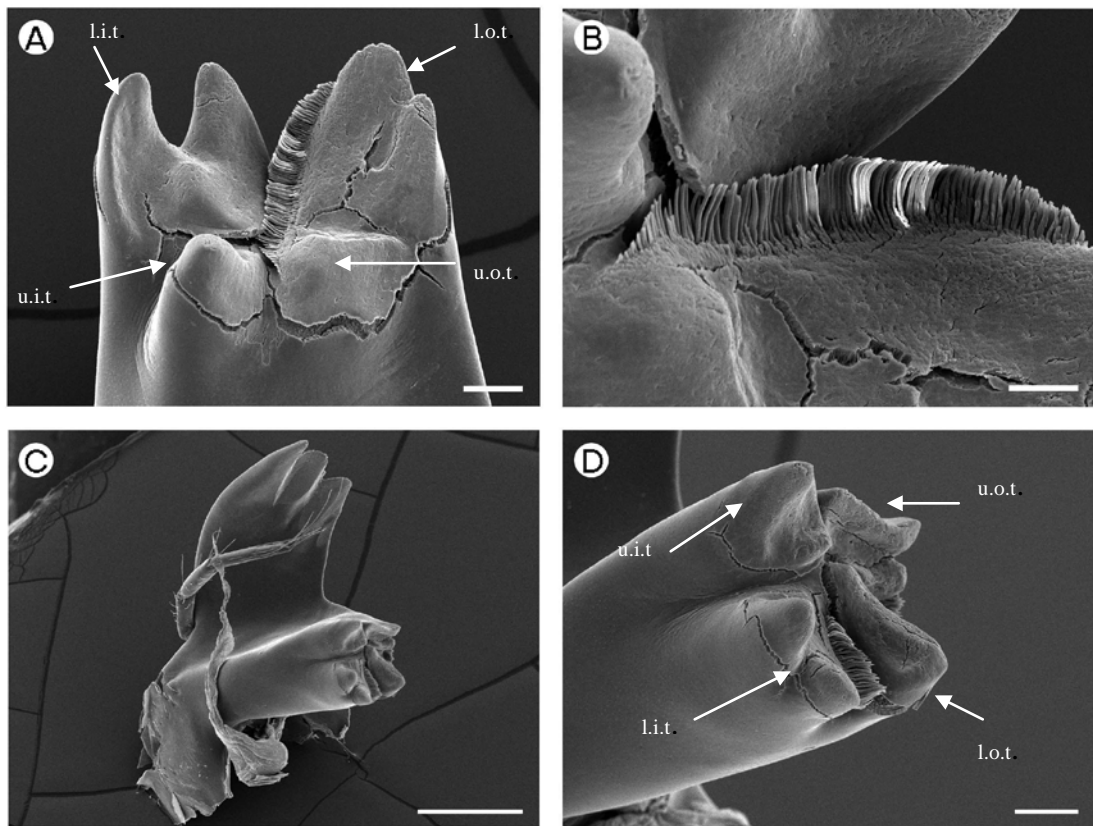


**Table 4.** Details of the distal ends of the pars molaris of each species examined.  
u.o.t.= upper outer tooth, u.i.t. = upper inner tooth, l.i.t. = lower inner tooth.

	<b>Right</b>	<b>Left</b>
<i>Palaemon macrodactylus</i>	Quadricuspid (Figure 1A)	Quadricuspid (Figure 1E)
<i>Macrobrachium nipponense</i>	Quadricuspid (Figure 2A)	Quadricuspid (Figures 2C-D)
<i>Pontonia pinnophylax</i>	Quadricuspid, with deep concavity (Figure 3B)	Quadricuspid, teeth flattened (Figure 3C)
<i>Periclimenaeus caraibicus</i>	Bifid, 2 acute ridges (Figure 4A-B)	Tricuspid (Figure 4C)
<i>Gnathophyllum elegans</i>	Single blade like tooth (Figure 5A)	Single blade like tooth (Figure 5D)
<i>Hymenocera picta</i>	2 recurved, spine-like teeth (Figure 4E)	2 recurved, spine-like teeth (Figure 4F)
<i>Desmocarid bislineata</i>	Ridged (Figure 6B)	Ridged (Figure 6D-F)
<i>Euryrhynchus wrzesniowski</i>	2 lobate ridges (Figure 7A-B)	Not examined
<i>Anchistioides antiguensis</i>	Quadricuspid (Figure 7E)	Tricuspid, u.o.t. and u.i.t. fused, wing-like, l.i.t. bifid (Figure 7F)



**Figure 1.** Palaemonidae (Palaemoninae): *Palaemon macrodactylus*, A) *pars molaris* of right mandible; B) Type I cuticular structures of right mandible; C) detail of Type I cuticular structures of right mandible; D) distally serrulate setae of mandible palp of right mandible; E) *pars molaris* of left mandible; F) lateral row of Type I cuticular structures of left mandible. Scale bars indicate 200  $\mu\text{m}$  (A), 100  $\mu\text{m}$  (E), 10  $\mu\text{m}$  (C and D) or 20  $\mu\text{m}$  (B and F). u.o.t. = upper outer tooth, u.i.t. = upper inner tooth, l.o.t. = lower outer tooth, l.i.t. = lower inner tooth.



**Figure 2.** Palaemonidae (Palaemoninae): *Macrobrachium nipponense*, A) *pars molaris* of right mandible; B) Type I cuticular structures of right mandible; C) left mandible; D) *pars molaris* of left mandible. Scale bars indicate 500  $\mu\text{m}$  (C), 100  $\mu\text{m}$  (A and D) or 50  $\mu\text{m}$  (B). u.o.t. = upper outer tooth, u.i.t. = upper inner tooth, l.o.t. = lower outer tooth, l.i.t. = lower inner tooth.

**Table 5.** Details of the mandibular cuticle structures of each species examined. u.o.t. = upper outer tooth, u.i.t. = upper inner tooth, l.o.t. = lower outer tooth, l.i.t. = lower inner tooth.

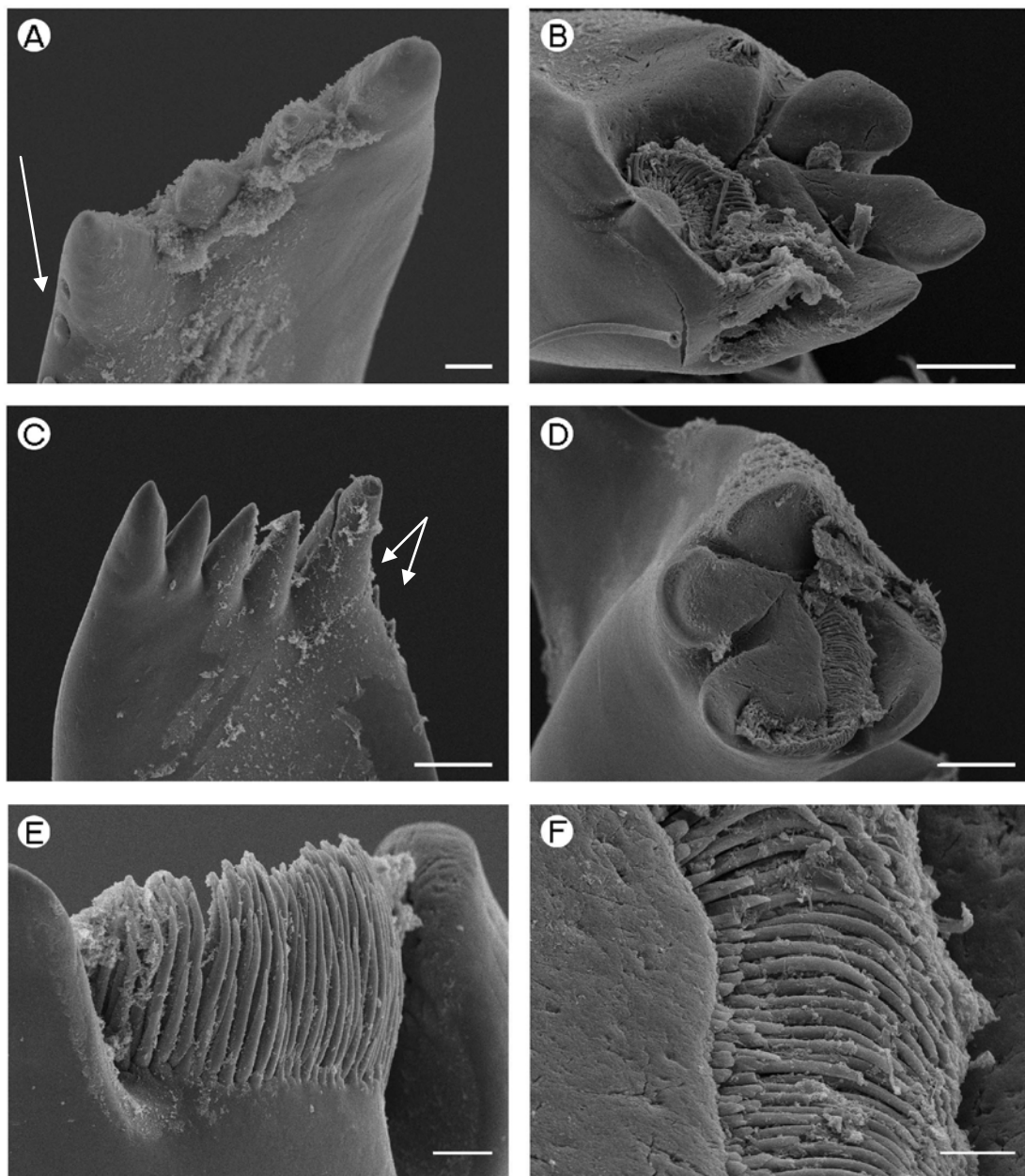
	<b>Right</b>	<b>Left</b>
<i>Palaemon macrodactylus</i>	Type I.	Type I
Figures 1B-C (Right)	Well-developed, row	In three discrete regions: row
Figure 1F (Left)	along inner margin of l.o.t, feebly developed row on u.o.t.	along inner margin of l.i.t., small tuft on outer margin of l.o.t., well-developed row on outer margin between l.o.t. and u.o.t.
<i>Macrobrachium nipponense</i>	Type I.	Type I.
Figures 2A-B (Right)	Well-developed row	Well developed row along
Figure 2D (Left)	along inner margin of l.o.t. and u.o.t.	inner margin of u.i.t. and as a small tuft on the outer margin between the l.i.t. and l.o.t.
<i>Pontonia pinnophylax</i>	Type I.	Type I.
Figures 3B, 3F (Right)	Confined to the	Well developed row, curled
Figures 3D-E (Left)	concavity in <i>pars</i> <i>molaris</i> tip. Arranged in a semicircle, in a rosette-like fashion.	around outer and inner margin of u.i.t., between l.i.t. and l.o.t. and along posterior margin.
<i>Periclimenaeus caraibicus</i>	Type II.	Type II.
Figure 4B (Right)	Present as a spine-like	Three distinct tufts one
Figure 4C (Left)	tuft in position of u.o.t.	between u.i.t. and l.i.t., and two on outer margin of l.i.t.
<i>Gnathophyllum elegans</i>	Type III.	As right mandible
Figures 5A-C (Right)	Very well developed	
Figure 5D (Left)	consisting of a single row that curls around to	

**Table 5.** cont.

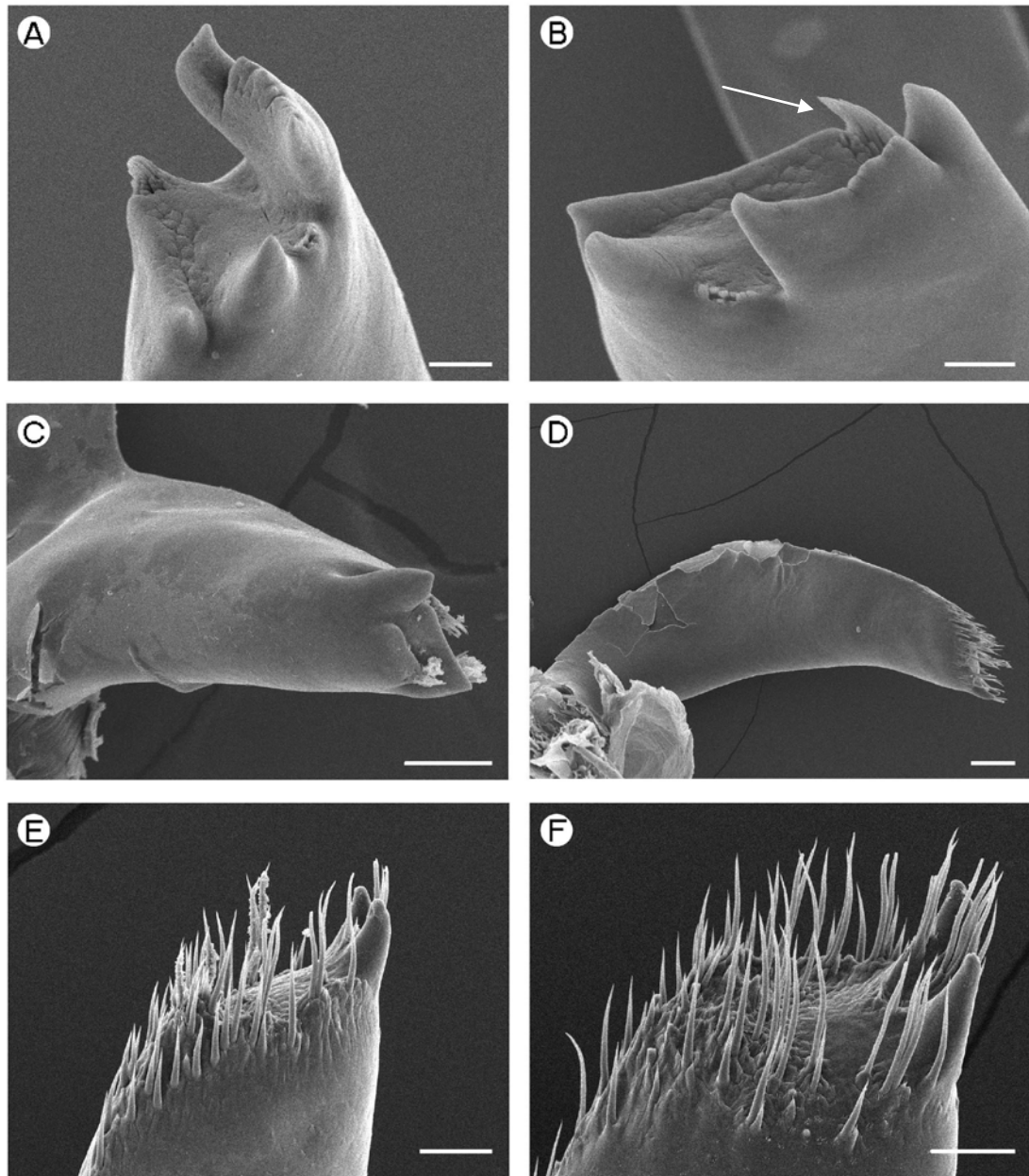
	<b>Right</b>	<b>Left</b>
	cover the entirety of the distal surface.	
<i>Hymenocera picta</i> Figure 4E (Right) Figure 4F (Left)	Type IV. Scattered	As right mandible
<i>Desmocarid bislineata</i> Figures 6B-C (Right) Figures 6D-F (Left)	Type V. Arranged into 12 equally spaced ridges giving a scalloped appearance. Median ridges longest and inner ridges notably shorter than outer ridges.	Type V. Ridges broader than those on right mandible, with rounded tips.
<i>Euryrhynchus wrzesniowskii</i> Figures 7A-C (Right)	Type I. Arranged in a transverse row.	Not Examined
<i>Anchistioides antiguensis</i>	Absent	Absent

### Discussion

Palaemonoid shrimps range from freshwater to marine habitats and from free-living species to obligate, or loose, associations with a variety of other invertebrates including cnidarians, echinoderms, molluscs and ascidians. The diversity of lifestyles and feeding strategies within palaemonoid shrimps has resulted a large range of morphological adaptations, including adaptations of the mouthparts and they therefore provide an ideal model group to test hypotheses related to the evolution of these structures. The hypotheses addressed here were that the structure of the mandible will convey information on the diet and/or phylogenetic relationships of the species.



**Figure 3.** Palaemonidae (Pontoniinae): *Pontonia pinnophylax*, A) *pars incisivus* of right mandible (denticles indicated by white arrow); B) *pars molaris* of right mandible; C) *pars incisivus* of left mandible (denticles indicated by white arrow); D) *pars molaris* of left mandible; E) Type I cuticular structures of left mandible; F) Type I cuticular structures of right mandible. Scale bars indicate 100  $\mu\text{m}$  (B and D), 50  $\mu\text{m}$  (C) or 20  $\mu\text{m}$  (A, E and F).



**Figure 4.** Palaemonidae (Pontoniinae): *Periclimenaeus caribicus*, A) *pars molaris* of right mandible; B) *pars molaris* of right mandible (spine-like tuft of Type II cuticular structures indicated by white arrow); C) *pars molaris* of left mandible. Hymenoceridae: *Hymenocera picta*, D) right mandible; E) distal end of *pars molaris* of right mandible; F) distal end of *pars molaris* of left mandible. Scale bars indicate 20  $\mu\text{m}$  (A and B), 100  $\mu\text{m}$  (D), 50  $\mu\text{m}$  (C, E and F).

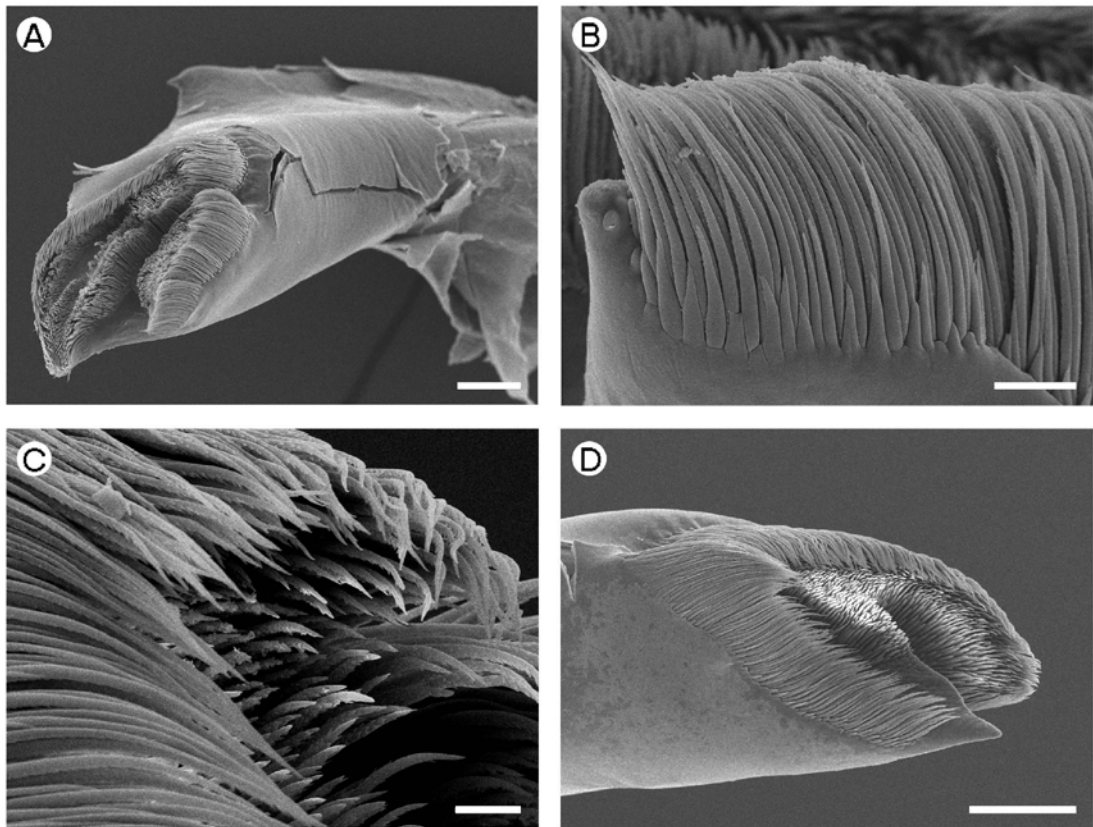
*General observations*

Whilst there is considerable variation in the mandible of palaemonoid shrimps noted in the literature, the most common form of mandible across the superfamily is a well developed *pars incisivus* and *pars molaris*, with mandibular palp being absent more often than present.

When present, the *pars incisivus* is of fairly constant form, differing only in its robustness and the number of distal teeth, this latter character often being also variable between the left and right mandibles. The *pars incisivus* of *Pontonia* is the most unusual of those investigated here in bearing a row of small denticles on the posterior border. These denticles are also present in most species of the closely related genera *Ascidonia*, *Dactylonia*, *Odontonia* but not in *Bruceonia* (see Fransen, 2002) but are not described in any other palaemonoid shrimp.

The detail of the *pars molaris* is more variable between genera than a review of the literature would suggest. This may be partly due to oversights in descriptions or because frequently only one mandible is described and illustrated. The right and left *pars molaris* in most cases showed significant differences in structure and are often configured such that there is a rough interlocking between the two sides when closed as also noted by Borradaile (1917). More startling is the wide degree of variation and intricacies in design of the cuticular structures. As mentioned, the presence of ‘setae’ or ‘bristles’ on the *pars molaris* has been noted in previous studies. However, these cursory mentions do not hint at the diversity in form, placement and arrangement witnessed in comparatively few species examined here.





**Figure 5.** Gnathophyllidae: *Gnathophyllum elegans*, A) *pars molaris* of right mandible; B) Type III cuticular structures of right mandible; C) detail of Type III cuticular structures of right mandible; D) *pars molaris* of left mandible. Scale bars indicate 20  $\mu\text{m}$  (B), 10  $\mu\text{m}$  (C), 100  $\mu\text{m}$  (A and D).

#### *Types of mandible and their presumptive function*

Based on the form of the mandible six broad types (Types A-F) can be recognised, which appear to relate to feeding mode or diet, although five of these types apply to single species only and the link with specialised food resources would require greater taxon coverage to include other species that share the similar diets.

*Type A mandible:* Well developed *pars incisivus* and *pars molaris*; *pars molaris* distally cuspidate; with Type I CS.

Type A mandibles are found in *Palaemon*, *Macrobrachium*, *Euryrhynchus* and *Pontonia*.

*Palaemon macrodactylus* is largely carnivorous with a preference for mysid and amphipod crustaceans (Sitts & Knight, 1979; Siegfried, 1982; González-Ortegón et al., 2010; Ashelby et al., in prep). The specific, natural diet of *Macrobrachium nipponense* has not been studied but it is likely that, as with most *Macrobrachium*, it is omnivorous with a tendency towards carnivory (Jayachandran & Joseph, 1989; Mantel & Dudgeon, 2004; Short, 2004). The diet of *M. hainanense* is dominated by insect larvae and gastropod molluscs (Mantel & Dudgeon, 2004) and a similar diet may be assumed for *M. nipponense*. Likewise the diet of *Euryrhynchus wrzesniowskii* has not been studied; however, Kensley and Walker (1982) provide some information on the diet of the related *E. amazoniensis* whilst Walker (2009) also gave information on the diet of this species and *E. burchelli*. Both species feed on a diverse prey range and can be regarded as omnivorous with a preference for live insect larvae. The diet of *Pontonia pinnophylax* is unclear. *Pontonia* inhabit lamellibranch bivalve, gastropod or ascidian hosts (Fransen, 2002; Marin & Anker, 2008). Richardson et al. (1997) concluded that the most likely food sources of *P. pinnophylax* were pseudofaeces (mucous-bound suspended particles rejected as food by the bivalve) or material collecting in the mantle cavity. Similarly, Aucoin and Himmelman (2010) observed *Pontonia mexicana* feeding on matter in mucus strings. Gut content analysis has revealed the presence of detrital material, plant material and crustacean exuviae (Richardson et al., 1997). Finally, Kennedy et al. (2001) concluded that *Pontonia* assimilated similar food to their bivalve hosts based on similar stable isotope carbon measurements. This similarity on the stable isotope measurements suggests another possibility not considered by those authors that the *Pontonia* feed on the bivalve host itself.

The hard-bodied, relatively large prey consumed by *Palaemon*, *Macrobrachium* and *Euryrhynchus* would require breaking down prior to ingestion. This suggests the requirement for a grinding mandible and the application of force. The cuspidate nature of the pars molaris of the Type A mandible is supportive of a grinding function. The abraded nature of many of the cuticular structures (particularly evident in Figures 1B-C) also supports this view. It would also be necessary for the shrimp to sense the prey between the mandibles to know what force is being applied to the prey, when the prey had been ground enough to ingest or when exoskeletons or shells of the prey had been broken. This is the presumed function of the Type I CS in the Type A mandible. The Type I CS are most similar to microtrichia. Microtrichia



are common in crustaceans, particularly in amphipods (e.g. Steele & Oshel, 1987; Oshel et al., 1988; Olyslager & Williams, 1993; Wong & Williams, 2009; Zimmer et al., 2009; Mekhanikova et al., 2012) and have also been noted in larval decapods (Pohle & Telford, 1981; Tziouveli et al., 2011). Typically microtrichia are thought to have a sensory function (Olyslager & Williams, 1993; Wong & Williams, 2009) and usually arise from a socket and terminate in a pore. A socket and pore are not evident in the SEM shots used here but this may be due to the resolution of the images and the abraded nature of many of the structures.

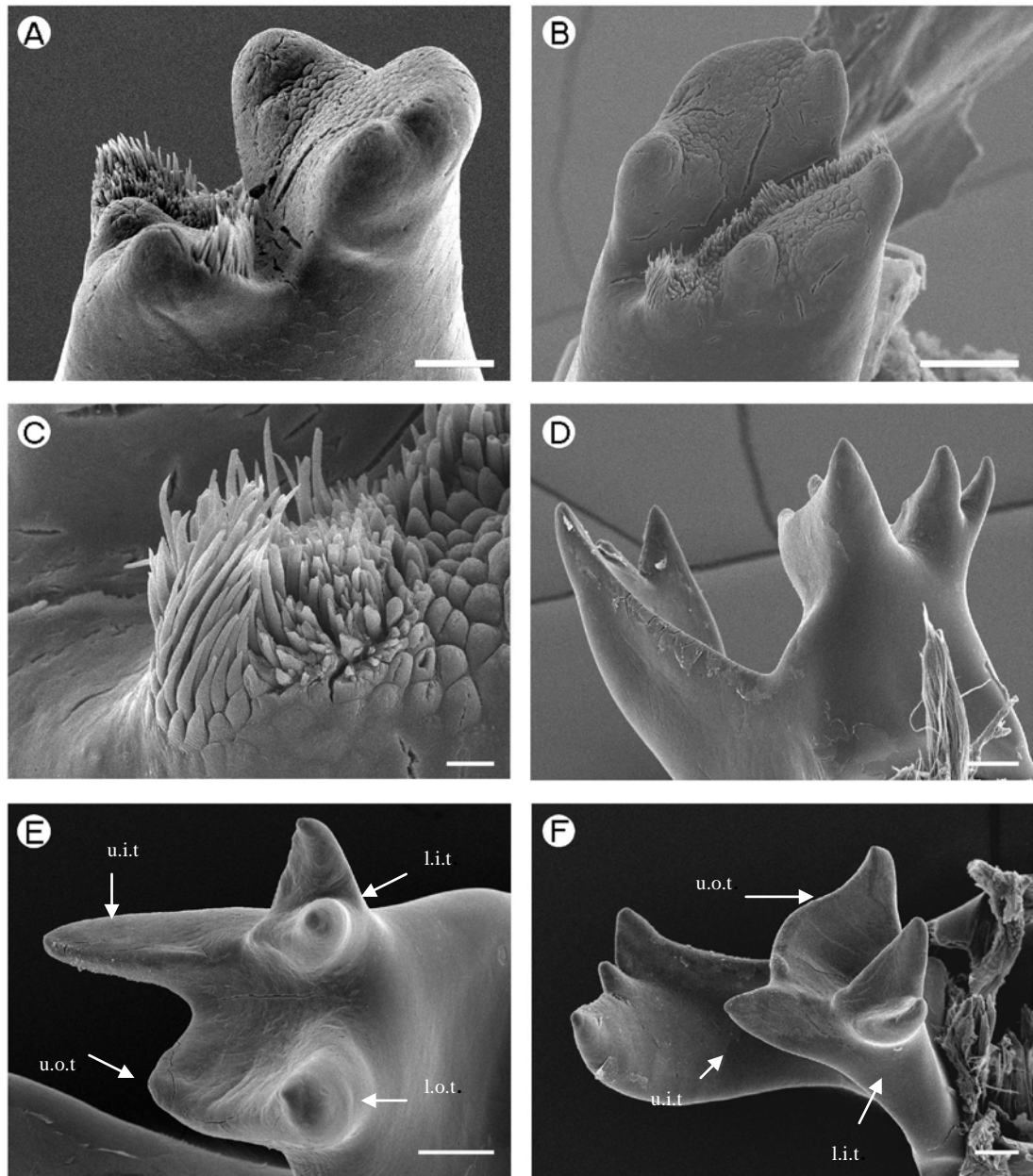
It is not clear how the presumed diet of *Pontonia* fits this mandible type. Assuming a pseudofaeces or mucus diet, there would not be the same requirement for grinding or mechanosensory structures. If the theory that the *Pontonia* feed on the bivalve hosts is correct then a shearing mandible would be necessary. This is partially supported by the form of the *pars incisivus* and the teeth of the right *pars molaris* which appear more acute than the other species included in this mandible type.

Based on examination of stomach content, Tsurumel (2008) suggests that *Typhlocaris* feed on bacterial mats and some small crustaceans. Feeding on bacterial mats may require specialised feeding structures, however, Figure 2F in Tsurumel (2008) show a mandible of very similar appearance to that of *Macrobrachium* and *Palaemon* which instead suggests a similar diet. This is further supported by the sensitivity of *Typhlocaris* to vibration (Tsurumel, 2008) which would aid in prey detection. Whether cuticular structures are present is not evident from the figures or descriptions in any *Typhlocaris* species.

*Type B mandible:* Well developed *pars incisivus* and *pars molaris*; *pars molaris* distally cuspidate; lacking cuticular structures.

The Type B mandible is only found in *Anchistioides antiguensis*. It differs from the Type A mandible chiefly through the lack of cuticular structures. The *pars molaris* is also distally flared in which is one of the defining characteristics of the family Anchistioididae and one of the few characteristics that is discernable in adults.

The only evidence as to the diet of *Anchistioides* was provided by Wheeler & Brown (1936) who report the presence of ‘worm setae’ in the stomachs of two specimens of *A. antiguensis*. The lack of any sensory apparatus may support preying on softer bodied animals which would require less force to break down.



**Figure 7.** Euryrhynchidae: *Euryrhynchus wrzesniowskii*, A) *pars molaris* of right mandible; B) *pars molaris* of right mandible; C) Type I cuticular structures of right mandible. Anchistioididae: *Anchistioides antiguensis*, D) right mandible; E) *pars molaris* of right mandible; F) left mandible. Scale bars indicate 10  $\mu\text{m}$  (C), 100  $\mu\text{m}$  (A, B, D, E and F). u.o.t. = upper outer tooth, u.i.t. = upper inner tooth, l.o.t. = lower outer tooth, l.i.t. = lower inner tooth.

*Type C mandible:* Well developed *pars incisivus* and *pars molaris*; *pars molaris* asymmetrical with 2 acute ridges on right and tricuspid on left; with Type II CS.

The Type C mandible is only found in *Periclimenaeus caraibicus*. There is a considerable degree of variation in the mouthparts of *Periclimenaeus* spp. reported in the literature and thus this type of mandible may not be standard for the genus. Variation in the development of the *pars incisivus* is noted as well as variation in the development or presence of cuticular structures but this latter difference may perhaps be attributable to oversight in the descriptions and figures due to difficulties observing this feature under standard microscopy. The ecological and phylogenetic significance of variation in features of the mandible amongst *Periclimenaeus* species warrants further investigation.

Đuriš et al. (2011) report that *Periclimenaeus caraibicus* feeds on the host sponges, noting the presence of spicules in the stomach and that the shrimp takes on the colour of the host sponge through assimilation of the sponge's pigments. The form of the mandible witnessed here is also suggestive of a specialised diet. The multidentate, serrated form of the *pars incisivus* would aid in the shredding of sponge fragments. The acute nature of the ridges of the right *pars molaris* may also aid in tearing. The sponge fragments may then be transferred into the groove of the right *pars molaris* into which the teeth of the left *pars molaris* can interlock to grind the sponge down. The groove may also help align unbroken spicules such that they enter the mouth in the correct orientation. The function and placement of the Type II CS in this mandible is difficult to explain. They appear similar in form to Type I CS and may therefore also be assumed to have a similar sensory function but their placement in discrete tufts would suggest that they may not provide thorough feedback. It is possible that these tufts of cuticular structures are the vestiges of those found in *Pontonia* and that they only have limited functionality. Type II CS may prove to be modified Type I structures but a lack of resolution and detail in the images prevents a firm conclusion on this and it seems best to recognise them as distinct for now.

Sponge feeding cannot be presumed to be a generalised diet for *Periclimenaeus* as some other members of this genus are associates of compound ascidians (Fransen, 2006) and so presumably have different feeding ecology which may be reflected in the form of their mandible, as discussed above.

*Type D mandible:* *Pars incisivus* strongly reduced to spine-like process; *pars molaris* with single blade-like tooth distally; with Type III CS.

The Type D mandible was found only in *Gnathophyllum elegans*.

Type D mandibles are highly modified and display a number of unusual features, most notably the reduction of the *pars incisivus* and the dense covering of Type III CS.

Little information is available on the diet of *Gnathophyllum*. Both Winkler (1973) and Bruce (1982) speculate that *Gnathophyllum* are predatory on echinoderms, however this hypothesis has not been confirmed. However, the highly modified form of all their mouthparts is suggestive a specialised food resource. During feeding, shrimps use the anterior mouthparts (maxillae and maxillipeds) to hold and manipulate food (Bauer, 2004). The operculate, calcified nature of the anterior mouthparts may not be able to manipulate food in the same way as the more flexible mouthparts found in most of the other genera examined here. The strongly reduced *pars incisivus* is suggestive that there is not a requirement for tearing or shredding of food items and the lack of a grinding surface on the *pars molaris* indicates that there is no requirement for breaking down food. Furthermore, the mandibles of *Gnathophyllum* are exceedingly small in relation to the body size of the shrimp and would be unlikely to be able to deal with large food items. Finally, the Type III CS appear highly flexible and cilia-like. These various adaptations would suggest that rather than large food items, *Gnathophyllum* feed on small particulate matter, mucus or fluids and the Type III CS are involved in movement of these food resources.

Although some species of Gnathophyllidae are commensals of echinoderms (Bruce, 1982), *Gnathophyllum elegans* is considered free living.. However, *Gnathophyllum* spp. do seem to form loose associations with echinoderms (S. De Grave, pers. comm.) and Bruce (1982) reports that *G. americanum* has been observed using its outer maxillipeds to browse on the extended papulae on the dorsal surface of asteroids. This, combined with the modifications to the mandible further supports the idea that *Gnathophyllum* feed on mucus or mucus entrapped particles, as has also been suggested for some other echinoderm associates such as *Periclimenes imperator*, *Lipkemenes lanipes*, *P. soror* and *P. pectiniferus* (Bruce, 1982).

*Type E mandible:* *Pars incisivus* absent; *pars molaris* bearing two recurved spine-like teeth distally; with Type IV CS.

The Type E mandible was found only in *Hymenocera picta*.

This type of mandible is differentiated from the Type D mandible through the complete absence of the *pars incisivus*, the presence of two recurved teeth on each mandible rather than a single blade-like tooth, and by the form and arrangement of the cuticular structures. As in the Type D mandible the *pars molaris* lacks a grinding surface.

*Hymenocera* and *Gnathophyllum* are so similar in the form of the mandible as well as their other mouthparts (a factor that has led to their previous inclusion in a single family) that it would be reasonable to assume a similar diet. However, Wickler (1973) noted that *Hymenocera* feed exclusively on starfish, particularly *Nardoa* and *Linkia* spp piercing the epidermis before extracting internal tissues.

The sparse arrangement of cuticular structures would also not be as effective at moving mucus or particles as those in the Type D mandible of *Gnathophyllum*. It seems likely, therefore, that the Type E mandible is a development of the Type D mandible in response to a dietary switch in *Hymenocera* (or its ancestors) from merely removing mucus from the echinoderms to actually preying on them. The paired teeth of the right *pars molaris* apparently interlink with those of the left and may take on the slicing role normally attributed to the *pars incisivus*.

*Type F mandible:* Well developed *pars incisivus* and *pars molaris*; *pars molaris* distally flattened and ridged; with Type V CS.

The Type F mandible was only noted in *Desmocaris*.

Type V CS are the most highly developed of all the cuticular structures noted in this study. They in turn dictate the form of this mandible type as the finger-like projections together form the ridged surface of the *pars molaris*. They appear to be flexible and may be regarded as shorter versions of the cilia-like Type III CS. A particulate or detritivorous diet may therefore be expected. This is consistent with the information provided by Powell (1977) who states that ‘normal feeding activity involves exploration of the surface of dead leaves etc....most of the food probably consists of fine particles...captive shrimps recoil from contact with live animals such as naidid oligochaetes and chironomid larvae; however they eagerly consume dead ones and therefore do not seem to be restricted to microphagy’. Although a strong *pars incisivus* is present for initial tearing, the Type F mandible does not have obvious grinding function and it is unclear how these carrion prey items would be broken



down prior to ingestion. Another possible function for the elaborate arrangement of cuticular structures in this mandible type is that they may help to filter particular matter.

#### *Systematic considerations*

The form of the mandible was considered by Thompson (1967) to be of significant importance in the phylogeny of the Caridea, with the ancestral state considered to be a fused *pars molaris* and *pars incisivus*, combined with a 3-segmented palp. Indeed, the recognition of several families, including some incorporated in this study, has partially been justified by the form of the mandible. The ridged nature of the *pars molaris*, which is presumed to be a primitive feature (Sollaud, 1911; Borradaile, 1917) is one of the characters used to define the family Desmocarididae (Borradaile, 1915; Powell, 1977) and the presence of a distally flared molar process of the mandible is one of the defining characteristics of the family Anchistioididae and one of the few characteristics that is discernable in adults (Chace, 1992). However, Fransen & De Grave (2009) concluded that whilst the form of mandible is of considerable value in the identification of carideans, its phylogenetic significance at the family level is uncertain. The inclusion of relatively few species in this study, encompassing less than 1% of palaemonoid diversity, albeit from the majority of palaemonoid families, will not uncover the complete range of forms of the mandible likely to be found in this group, meaning that the results of this study should be regarded as indicative rather than absolute. Furthermore, the analysis of a single character in isolation cannot hope to resolve systematic relationships, rather an integrative approach, including novel characters and possibly also molecular data is advised (Li et al., 2011). Nevertheless some preliminary observations on the structure of the mandible in relation to currently accepted phylogenies can be made.

The six mandibular types proposed here do not reflect currently accepted relationships within the Palaemonoidea. As many of the groupings are based on single taxa they may actually imply species specific differences or, perhaps reflect over-splitting of mandibular types in this study.

The closely related genera *Palaemon* and *Macrobrachium* have the same general structure of the mandible (Type A); however, the other genera with this form of mandible are more difficult to explain from a phylogenetic point of view. *Pontonia*

shares a greater affinity to *Gnathophyllum*, *Hymenocera* and *Periclimenaeus* (Mitsubishi et al., 2007; Bracken et al., 2009) than to *Palaemon* or *Macrobrachium* whilst *Euryrhynchus*, considered to be an ancient lineage (De Grave, 2007), represents a sister group to *Desmocarid* (see Bracken et al., 2009). *Palaemon* and *Macrobrachium* both also possess a mandibular palp. The traditional view of the mandibular palp is that the presence of a three segmented mandibular palp represents the primitive condition in Caridea (Thomson, 1967) with a reduction in the number of segments and subsequent loss in more derived lineages. However, the presence or absence of a mandibular palp has been demonstrated to convey very limited phylogenetic information and is not a consistent character in Palaemonidae, varying even within a species (Ashelby et al., 2012).

Although classified into two different mandible types here (Type D and Type E), the mandibles of *Gnathophyllum* and *Hymenocera* are linked through the reduction of the *pars incisivus*, a feature that is variable in the gnathophyllid genus *Gnathophylloides* (see Chace & Bruce, 1993). Mitsubishi et al. (2007) and subsequently Bracken et al. (2009) demonstrated that Hymenoceridae and Gnathophyllidae represent a derived lineage within the Pontoniinae. The mouthparts present many of the definitive morphological characters of this lineage. The gradual reduction of the *pars incisivus* witnessed in the Gnathophyllidae and Hymenoceridae is also a feature demonstrated in several Pontoniinae taxa indicating the potential plasticity of this character within the subfamily. Reduction of the *pars incisivus*, although to a lesser degree, is also noted in *Calathaemon* (currently Kakaducarididae). A gradual reduction of the *pars incisivus* at family level is indicated by Burukovsky (1986) with Gnathophyllidae being intermediate in form between Palaemonidae and Crangonidae. However, these latter families, and the Eugonatonotidae in which the *pars incisivus* is also absent, are not closely related (Mitsubishi et al., 2007; Bracken et al., 2009; Li et al., 2011) suggesting that the loss of the *pars incisivus* has occurred several times in the evolution of the Caridea.

This study has demonstrated that the form of the mandible is much more complex than previously thought. The traditional view that the *pars molaris* is used solely for the grinding of food seems a gross oversimplification and in some species (e.g. *G. elegans*, *H. picta*) the arrangement and form of the teeth would suggest that it does not grind at all. The form and arrangement of cuticular structures at the distal end of the *pars molaris* shows a particularly high degree of variation. The five types

of cuticular structures recognised in this study are presumed to have different functions related to food sources, which is contrary to the findings of Storch et al. (2001) who found no link between the morphology of the mouthparts and food items.

Some evidence of evolutionary relationships is conveyed through the broad structure of the mandible but the detailed structures witnessed in this study do not reflect the evolutionary relationships in the Palaemonoidea suggested by previous phylogenetic reconstructions (Mitsubishi et al., 2007; Bracken et al., 2009; Li et al., 2011). With such a diversity of lifestyles represented by the Palaemonoidea, particularly within the subfamily Pontoniinae, further studies including other genera are likely to reveal an even greater diversity of mandible morphology than revealed by the present study.

### Acknowledgements

Jack Howe is thanked for taking and allowing us to use the SEM shots used in figures 1B-D. Thomson Unicmarine partially supported the work of the first author.

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## Chapter 5: Human-mediated spread of *Palaemon*

1. The global invader *Palaemon macrodactylus* (Decapoda, Palaemonidae): an interrogation of records and a synthesis of data.  
[Published in: *Crustaceana* 86(5): 594-624]
2. Diet analysis indicates seasonal fluctuation in trophic overlap and separation between a native and an introduced shrimp species (Decapoda: Palaemonidae) in the Tidal River Thames.



**The global invader *Palaemon macrodactylus* (Decapoda, Palaemonidae): an interrogation of records and a synthesis of data**

**Abstract**

In the latter half of the 20<sup>th</sup> Century and the early part of the 21<sup>st</sup> the Asian shrimp species, *Palaemon macrodactylus* began being reported from several world-wide locations. Literature records of *Palaemon macrodactylus* have been collated here and corroborated through examination of material, where possible. Material from each main geographic region, with the exception of northeast Atlantic, has been verified as *P. macrodactylus* but records from Taiwan and Darwin do not refer to *P. macrodactylus* and some records still require verification in the absence of material. The data show that, in most cases, the first occurrence of *P. macrodactylus* in a region is several years prior to the detection of the species, further highlighting the difficulty in early detection of invasive species. Biological, ecological and physiological aspects of the species are summarised to try to gain an understanding of why the species has become so successful at colonising other areas but the factors favouring the introduction of *P. macrodactylus* over other species of *Palaemon* are still unclear as many of *P. macrodactylus*' traits are common to other species of the genus also. Information on larval tolerances may provide further clues for the success of *P. macrodactylus*. We hypothesise that the global distribution of the species has been achieved through a combination of at least three primary introductions from Asia and three secondary introductions from other non-native populations, whilst the origin of the Argentinean population remains unclear. Small-scale secondary introductions have likely aided spread within a region. Regions at risk of invasion by *P. macrodactylus* include the Baltic Sea, southern Norway and South Africa, whilst further spread within regions it already occupies should be expected.

**Introduction**

The human-mediated global transport of marine and estuarine organisms has been occurring ever since man began traversing the oceans and is often cited as one of the greatest threats to biodiversity (Coblentz, 1990; Wilcove et al., 1998; Mooney &

Cleland, 2001; Simberloff, 2010). With increased shipping and decreased transit times as well as the global effects of climate change the rate of reported introductions appears to be rising (Cohen & Carlton, 1998; Occhipinti-Ambrogi, 2007). This is paralleled with increased awareness through publication of records in the scientific literature, the internet and other non-scientific media, as well as the establishment of environmental monitoring programs in many countries, which probably aids the detection of non-native species. Nevertheless, detection of an introduced species in a region often remains largely a chance occurrence, especially at low population densities or where the invader occupies a cryptic niche and the true number and distribution of invasive species will likely never be known.

Generally, successful introductions are from similar latitudes (Eno et al., 1997) and certain species seem to be biologically predisposed to successful introductions enabling them to achieve near global distribution in suitable thermal regimes (e.g. Critchley, 1983; Carlton & Cohen, 2003; Ashton et al., 2007; Goldstein et al., 2011). With the caveat that taxonomically well known and relatively large organisms are more likely to be recognised as introduced, crustaceans are amongst the most successful groups for introductions in aquatic environments (Ashton et al., 2007) and amongst these the Decapoda are well represented. Rodríguez and Suárez (2001) listed 86 marine and freshwater decapods dispersed from their natural ranges up to that date, including 20 caridean shrimps, and further introductions of shrimps continue to be reported (e.g. Emmet et al., 2002; De Grave & Ghane, 2006; Salman et al., 2006; Zare et al., 2010; Pachellet et al., 2011; Taylor & Komai, 2011; De Grave & Mann, 2012; Almeida et al., 2012). In recent years, the Oriental Shrimp, *Palaemon macrodactylus* Rathbun, 1902, has become one of the most widely reported non-native aquatic species, with literature records from most temperate and some tropical biogeographical provinces. Due to discrepancies in ecology and habitat in some published accounts of *P. macrodactylus*, the true distribution of the species remains uncertain and a reappraisal of these reports is required.

In this study we re-evaluate the reported distribution of the species and synthesise the available data on possible modes of transport, potential impacts, factors favouring the spread of the species and suggest other regions at risk of invasion by *P. macrodactylus*.



## Material and Methods

Literature records on the biology, life history and occurrence of *P. macrodactylus* were collated and scrutinised. Literature was sourced through a combination of searches in ScienceDirect, using various search terms for non-native species, keyword searches on *Palaemon macrodactylus*, as well as systematic searches through journals specialising in invasion biology and by backtracking through the bibliographies of the obtained literature. Where possible, specimens cited in these papers as well as additional specimens from the same geographic regions were examined. Adult specimens from each geographic region from which *P. macrodactylus* has been reported were available for examination, with the exception of eastern U.S.A., a list of examined material is provided in the appendix.

All specimens and literature illustrations were subjected to a rigorous morphological examination and compared with the key morphological characters detailed in the type description (Rathbun, 1902), the description of Japanese material in Kubo (1942), as well as the redescription of the species by Newman (1963). The type material held at USNM, Washington (USMN 26162) was not consulted during this study but was studied by Newman (1963) to confirm the identity of the San Francisco Bay specimens. In the absence of material from the eastern U.S.A., the figures of specimens from New York provided by Warkentin and Rachlin (2010) were consulted to confirm the identity of these specimens.

The following features were considered to be diagnostic: carapace with antennal and branchiostegal teeth and branchiostegal groove; branchiostegal tooth submarginal, branchiostegal groove closely applied to tooth. Rostrum slender, only weakly expanded ventrally, straight or slightly upcurved with 9-15 dorsal teeth, usually three of which are behind the posterior edge of the orbit; distance between first and second tooth between 1.5 and 2 times as long as that between second and third teeth; distal portion (up to one fifth) unarmed; 3-5 ventral teeth, tip bifid; ventral margin with double row of plumose setae. Mandible usually with three-segmented palp. Dorsal flagellum of the antennula approximately equal in length to antennular peduncle, fused for about 20% of its length. Chela of second pereiopod equal to or slightly longer than carpus; fingers of chela about 0.7 times as long as palm. Dactylus of pereiopods 3-5 slender, about 0.9 times as long as carpus. Fifth abdominal pleuron

with small distoventral tooth. First pleopod of male without marginal appendix on endopod.

Institutional abbreviations used in the appendix are as follows: AM (Australian Museum, Sydney), NHM (Natural History Museum, London), NMSZ (National Museums of Scotland, Zoological Collection), NTM (Northern Territories Museum, Darwin), NTOU (National Taiwan Ocean University), OUMNH-ZC (Oxford University Museum of Natural History, Zoological Collection), RMNH (Rijksmuseum van Natuurlijke Historie (= Naturalis), Leiden).

## Results and Discussion

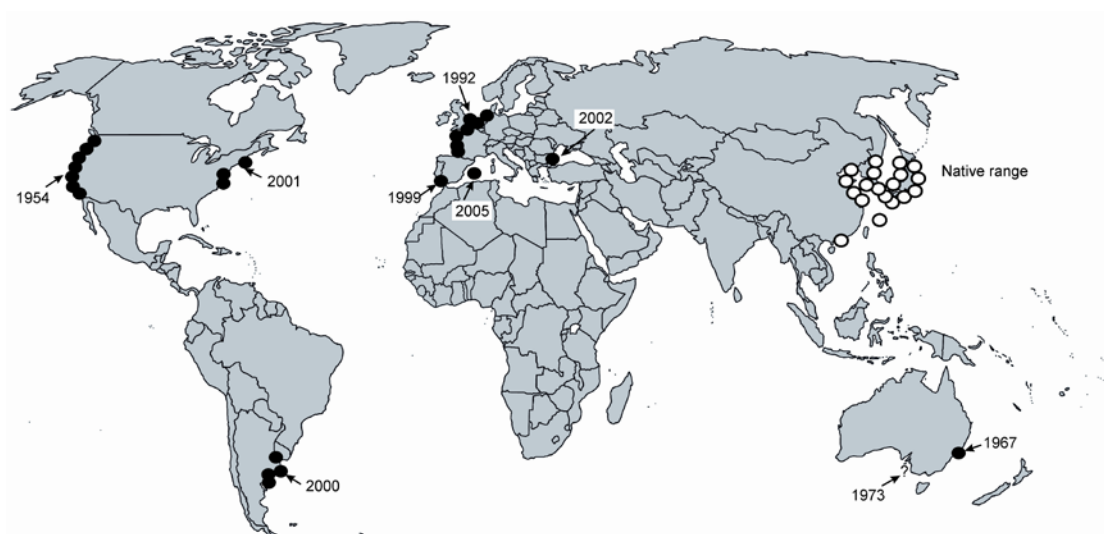
### *Invasion History*

*Palaemon macrodactylus* has been globally introduced to at least six discrete regions (Figure 1) indicating the occurrence of at least six invasion events for the species, although multiple introduction events in some regions are also hypothesised below. A chronology of the earliest documented occurrences of the species in each region is presented in Figure 1; however, whether this represents the true sequence of these introductions remains a matter of speculation. In all regions populations have invariably become established and abundant prior to first detection and in most areas of introduction the occurrence of the species has been antedated by examining archived material. For example, in Europe the species was first recorded by Ashelby et al. (2004) and Cuesta et al. (2004), but had been already present for over a decade before (Worsfold & Ashelby, 2008). This is consistent with the observations of Carlton (1985) who noted that dates of introduction of a species are rarely coincidental with date of detection.

*Palaemon macrodactylus* was first noted outside of its native north-east Asian range in San Francisco Bay in 1957, but was possibly present in the region since 1954 (Newman, 1963). It has since spread to many other areas including Australia in the 1970s (Buckworth, 1979), Atlantic and North Sea coasts of Europe since 1992 (Ashelby et al., 2004; Cuesta et al., 2004; d'Udekem d'Acoz et al., 2005; Béguer et al., 2007; González-Ortegón et al., 2007; Worsfold & Ashelby, 2008; Chícharo et al., 2009), Argentina in 2000 (Spivak et al., 2006) and the Black Sea in 2002 (Micu &

Niță, 2009; Raykov et al., 2010). Most recently it has been reported in estuaries surrounding New York City where it has been present since at least 2001 (Warkentine & Rachlin, 2010) and larval records off Mallorca (Torres et al., 2012), based on 2005 and 2010 samples.

Within the last decade the number of reports of *Palaemon macrodactylus* from new areas has dramatically increased. Whether the rate of introduction is genuinely increasing or this apparent trend represents increased detection of the species due to heightened awareness or increased sampling efforts is unclear.



**Figure 1.** Global distribution of *Palaemon macrodactylus* Rathbun, 1902. Native range is indicated by open circles, invasive ranges by black circles. For each region, the earliest record of occurrence is indicated; the Adelaide record is indicated by a question mark, as no specimens could be examined during the present study.

#### *Native Range*

Rathbun (1902) described *Palaemon macrodactylus* from a number of specimens from localities in Japan and Korea and it has since been reported from China (Li et al., 2007) and Russia (Kobjakova, 1967). In Japan, the species is distributed from Hokkaido to Tanegashima Island in the northern Nansei Islands (T. Komai, pers. comm.), but also occurs further south to Okinawa (Shokita, 1979). In her original description of the species, Rathbun (1902) mentions Japanese records from Aomori (Type Locality), Matsushima and Nagasaki. Subsequent Japanese

records are from Sagami Bay (Parisi, 1919), Tokyo Bay, Atumi Bay (Nisiura-mura, Aichi Prefecture) and Hachirōgata (Kubo, 1942), Obitsu River Estuary, (Kisarazu, Chiba Prefecture), Kii Peninsula (Mie Prefecture) and Sado Island (this study, see appendix).

Kobjakova (1967) reports the occurrence of *P. macrodactylus* in Posjet Bay and Peter the Great Bay in the Russian Far East, with Dolganova et al. (2008) also recording the species in Peter the Great Bay from fish stomachs. Further, previously unreported, samples from Peter the Great Bay at Mys Ostrovok Fal'shivvy and Vostok Bay are held at Natural History Museum and Institute, Chiba, Japan (T. Komai, pers. comm.).

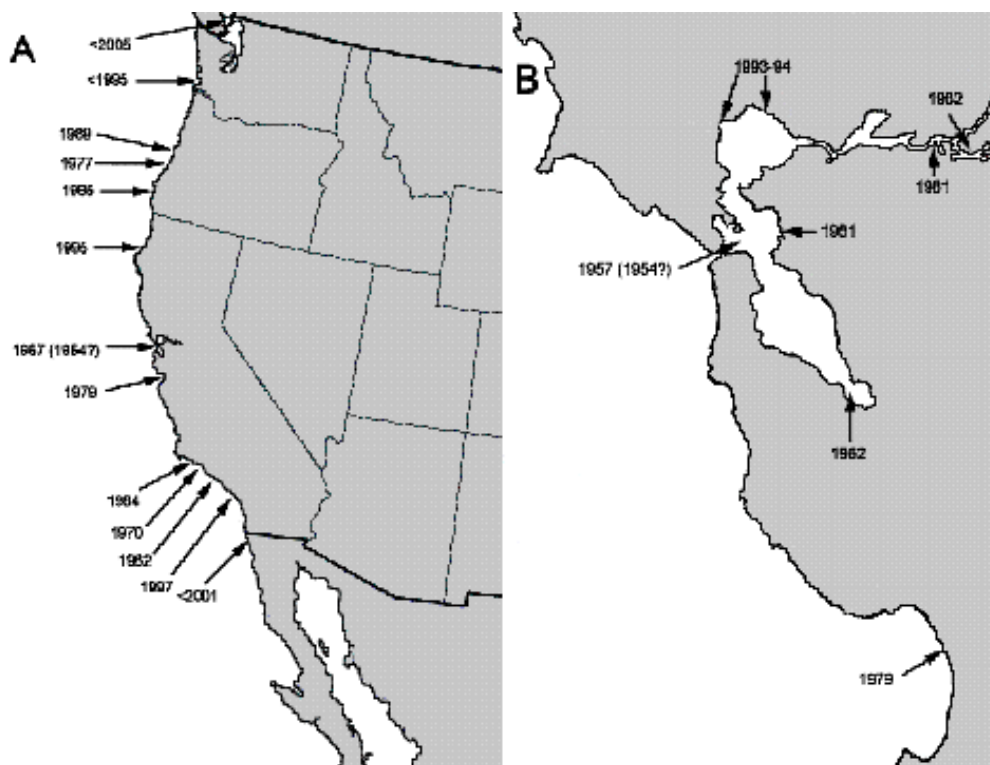
Rathbun (1902) included material from Gensan in the Democratic People's Republic of Korea and Fusan (now Busan) and Chemulpo (now Inch'on) both in the Republic of Korea in her description of *Palaemon macrodactylus*. Further material from Busan has been examined in this study as well as specimens from Yangpo, Gyeongbuk, in the south-east Republic of Korea, and the species is considered to be abundant along southern coasts (J.N. Kim, pers. comm.).

Quan et al. (2012) list *P. macrodactylus* as a dominant component of an artificial oyster reef in the Yangtze River, Jiangsu Province, whilst Li et al. (2007) summarise the general distribution of *P. macrodactylus* in China. Here it occurs south as far as Zhejiang Province with a further record from Guanghai, Guangdong Province (Li, pers. comm.). This latter record is slightly removed from the closest record to the north representing a gap in its reported distribution in southern China. As Guanghai is a large fishing port it is possible that the Guangdong record represents a short-range introduction, but more data are required to support this hypothesis.

#### *North East Pacific – 1950s*

The first record of *P. macrodactylus* outside of its native range is from San Francisco Bay (Newman, 1963). Although not actually recorded until 1957, Newman (1963) considered it likely to have been present in the region since at least 1954, possibly being transported by ships returning from the Korean War. This view may be supported by the fact that it was abundant enough by 1957 to appear in commercial shrimp catches. By 1961 it was present throughout much of the Bay and upstream as far as Antioch (Newman, 1963; Figure 2B). Since these early records, *P.*

*macrodactylus* has achieved a large range along Pacific North American coasts and its spread, particularly in the years immediately following its introduction has been linked to the accidental or deliberate release by anglers using the species for bait (Carlton, 1985; Williams, 1997; Figure 2A). Currently the range of the species along this coast is from Boundary Bay, British Columbia in the north southwards to the Tijuana Estuary (San Diego County), California (Figure 1, 2A).



**Figure 2.** North West Pacific records of *Palaemon macrodactylus* Rathbun, 1902. A, earliest occurrence in each state or geographic area; B, detail of the San Francisco Bay area.

Following the discovery of *P. macrodactylus* in San Francisco Bay, it apparently dramatically extended its range within California over the next five years (Figures 2A-B) when it was found in Los Angeles Harbour in 1962 (Cohen & Carlton, 1995). This may be indicative of either a secondary introduction from San Francisco Bay or a further primary introduction from Asia (Standing, 1981). Alternatively, perhaps the species achieved this extension through natural dispersal and went undetected in the intermediate part of this range. By the late 1970s *P.*

*macrodactylus* had been found in Santa Monica Bay (Cohen & Carlton, 1995). Standing (1981) found the species in Elkhorn Slough in 1979 whilst Wicksten (1989) reported on 3 further specimens collected in Malibu Lagoon in 1984. More recently, *P. macrodactylus* has been found in Humbolt Bay in 1995 (Cohen & Carlton, 1995; Wonham & Carlton, 2005), and the Napa River and Petaluma River between 1993 and 1994 (Cohen & Carlton, 1995) whilst Williams (1997) reports *P. macrodactylus* as abundant in beach seines in the Los Peñasquitos Lagoon. The confirmed southernmost limit of the species in western North America is the Tijuana Estuary (Williams et al., 2001; Trostler et al., 2010). In the absence of material for examination, a record from Bahia de Los Angeles (Pacheco-Ruíz et al., 2008) is considered suspect, as the region is likely too warm for *P. macrodactylus* (J. Carlton, pers. comm.).

In Oregon, *P. macrodactylus* was first recorded from Coos Bay in 1977 and then from 1986 onwards (Carlton, 2000; Ruiz et al., 2000). It is likely that the species arrived in Coos Bay some time prior to 1977 and that the population persisted between 1977 and 1986 but no sampling is known to have taken place in the intervening period (J. Carlton, pers. com.). Chapman (1988) made an incidental record of *P. macrodactylus* from the Oregon Oyster Company, Yaquina Bay whilst sampling for non-native amphipods. J. Chapman (pers. com.) informed us that he has also found the species in the Rogue Estuary in 1985 but that, despite further sampling in those estuaries, particularly the Yaquina, he has not recorded the species since.

Jensen (1995) reports *P. macrodactylus* occurring in Willapa Bay (Figure 2A), which is the only published record for Washington State to date. Cohen et al. (1998) did not find *P. macrodactylus* during their surveys of Puget Sound, but Lamb and Hanby (2005) provide a record from the mouth of the Nicomekl River, Boundary Bay, British Columbia, Canada suggesting its arrival in the area is a relatively recent event. This record from Boundary Bay provides the most northern report in the region (Figures 1, 2A).

#### *Australia – 1960-1970s*

The historical occurrence and current distribution of *Palaemon macrodactylus* in Australia has been, and partly remains, unclear. The earliest published record of the species is in Williams et al. (1978) from an unspecified location in South

Australia, based on a personal communication by T. Walker. Buckworth (1979) refers to specimens collected by T. Walker of the species from Torrens Island, Power Station, close to the Port of Adelaide, likely to be the source of the record in Williams et al. (1978). Walker and Poore (2003) state that the identity of specimens from two locations in Australia had been confirmed by L.B. Holthuis and at our request, C. Franssen (NCB-Naturalis, Leiden) examined the correspondence archive of Holthuis. This revealed that a single specimen was sent by T. Walker to Holthuis for identification, collected from “*Ulva* plus other weeds on car tyres used as moorings near the Torrens Island Power Station” by T.M. Walker and P. Zed on 20 August 1973. The current whereabouts of this specimen are not known, and it is not present in the NCB-Naturalis collection, but Holthuis in a letter to T. Walker (in lit., 28 December 1976) did confirm the specimen to be *P. macrodactylus*. At Torrens Island, specimens were collected at a single location and as indicated in Walker’s letter to Holthuis (in lit., 10 December 1976) were confined to a region of thermal pollution (“thermal pollution caused by the power station has lifted the water temp. to 33°C.”). Two lines of circumstantial evidence potentially suggest that a different species could be involved. Currently *P. macrodactylus* throughout its range, is not encountered in heated effluent water and the stated temperature is likely too high for the species to thrive. Furthermore, the colour pattern given by Walker and Poore (2003) for *P. macrodactylus*, which according to T. Walker (pers. comm.) was based on the specimens from Torrens Island, is not consistent with that reported from other regions. However, we have no reason to doubt the identification of the single specimen by Holthuis and accordingly accept that a population was present in 1973 at Torrens Island. Further searches in Australian and other museums have revealed no additional material to substantiate this record nor any more recent material, and as in neither Pollard and Hutchinson (1990) nor Wiltshire et al. (2010), we can currently not further corroborate the record, nor the continued existence of the species in South Australia. More recently, Wear and Tanner (2007) recorded *P. macrodactylus* in a study from around a sewage outfall in the Gulf of St. Vincent, South Australia. Whilst no longer available for examination, specimens cited in this paper were subsequently re-identified as *Palaemonetes australis* Dakin, 1915 (J. Tanner, pers. comm.).

Buckworth (1979) in his MSc thesis, reported specimens from Vales Point Power Station at Lake Mannering, believing the species to have been introduced

either in, or shortly before, 1977. These records have been repeatedly cited (e.g. by Pollard & Hutchinson, 1990; Ashelby et al., 2004; Spivak et al., 2006; González-Ortegón et al., 2007) as the only verified occurrence of *P. macrodactylus* in Australia. Several of the specimens cited by Buckworth (1979) from Lake Mannering have been re-examined during the present study (see Appendix). *Palaemon macrodactylus* has also been reported as established in the Tuggerah Lakes System (N.S.W.) at Munmorah Power Station (T. Walker pers. comm. in Buckworth, 1979), adjacent to Lake Mannering. This latter observation is the second Australian location referred to in Walker and Poore (2003) as being confirmed by Holthuis. Indeed, the same letters in the Holthuis archive as referred to above, mention a single specimen from Lake Munmorah, collected by J. Clark in August 1974 sent for identification by T. Walker and confirmed to be *P. macrodactylus* by Holthuis.

Buckworth (1979) postulated that *P. macrodactylus* was introduced to Australia in a similar way to the San Francisco Bay population but that the Lake Mannering population was derived from Lake Munmorah, as Lake Mannering receives water from Lake Munmorah via Munmorah Power Station. However, an ovigerous female specimen examined during the course of this study collected from the Hunter River in 1967, held in the collections of the Australian museum (AM P 16203; see Appendix), now provides the earliest reported occurrence of the species in Australia and offers an alternative hypothesis for the introduction of the species to Australia. We postulate that the species was introduced at the Port of Newcastle shortly before or during 1967 and subsequently spread to Lake Macquarie, on the southern shore of which the Vales Point Power Station is situated, and then slightly further south to the Tuggerah Lakes System. This is perhaps corroborated by the fact that there was an increase in shipping, particularly of coal from this port in the 1960s and 1970s (data from NCP, 2012). The Port of Newcastle is situated about 20km to the north of the entrance to Lake Macquarie and about 50km to the north of the entrance to the Tuggerah Lake System. These distances are well within the natural dispersal distances proposed by Lavesque et al. (2010) based on its European spread and could have been easily achieved in the 10 years that elapsed between the introduction to Newcastle and the discovery at Vales Point.

As is the situation in South Australia, no further verified records exist for New South Wales and the current status of the species in the region is unclear. The Lake Mannering site sampled by Buckworth (1979) has now been completely land filled



(R. Buckworth, pers. comm.) and it is unknown whether a population remains present in Lake Munmorah to this day. The habitat in Lake Macquarie and the Tuggerah Lake System does appear suitable to sustain a population, thus the lack of recent records (both published and unpublished) could either be attributed to a lack of sampling in the area or that the population has not persisted in N.S.W. to the present day. The latter would seem unlikely, as in all other areas from where the species has been reported, populations have always persisted after the initial reports and we herein speculate that the species is still present in Lake Macquarie and surrounding areas.

A further Australian record of *P. macrodactylus* was made from Darwin Harbour, Northern Territory by Bruce and Coombes (1997). The specimens reported by Bruce and Coombes (1997) were re-examined here (see Appendix) and found to be juveniles of a species of *Macrobrachium* and we therefore discount the occurrence of *P. macrodactylus* in northern Australia.

#### *Tropical West Pacific (Taiwan) – 1984*

Chan and Yu (1985) reported *P. macrodactylus* in their review of Taiwanese *Palaemon*. However, a number of discrepancies in morphology, colour pattern and habitat suggested that this record likely refers to a different species. In particular, Taiwan is situated in a higher temperature range from which the species has otherwise been reported and the records from fully marine conditions on rocky shores would be an unusual habitat for *P. macrodactylus*, but more importantly the figures provided in that report do not appear consistent with *P. macrodactylus* as illustrated in Kubo (1942) and Newman (1962). Additionally, the colour pattern is described as consisting of definite longitudinal stripes of colour on the carapace, which are not found in *P. macrodactylus*. Of the two lots reported as *P. macrodactylus* by Chan and Yu (1985), one was not available for examination (rocky shore, Pa-Tou-Tsu, Keelung City, 3 June 1984); however re-examination of some of the specimens from the second lot (aquaculture pond, Donggang, Pingtung County; 7 June 1984), as well as additional specimens from the same locality (see Appendix) confirms the suspicion that they are not *P. macrodactylus* and shows them to belong to a form of *P. serrifer* (Stimpson, 1860). Furthermore, recent, extensive sampling in several locations in Taiwan, failed to find any *P. macrodactylus* (S. De Grave, pers. comm.) and we therefore discount its occurrence in Taiwan.

*North East Atlantic – 1990s-2000s*

*Palaemon macrodactylus* occupies a large geographic range along the Atlantic coasts of Europe, seemingly having colonised most (but not all — see Lavesque et al., 2010) suitable habitats in this region, south of the southern North Sea (Figures 3A-B). It is currently found between Germany and southern Spain. The earliest reported occurrence of the species for Atlantic coasts of Europe is from the River Thames, UK in November 1992 (Worsfold & Ashelby, 2008) when a single specimen was reported amongst many specimens of the native *P. longirostris* H. Milne Edwards, 1837 collected as part of a long-term study at West Thurrock Power Station by Attrill et al. (1999). As only a single specimen was encountered it may be hypothesised that this individual was part of the initial arrival phase of the colonisation of Europe. Attrill et al. (1999) indicate that samples obtained between 1989 and 1992 were abnormal due to drought conditions prevailing in the region at that time which increased the concentrations of heavy metals and would cause changes to the salinity regime in the estuary. The species was abundant in the River Thames by 2006 (Worsfold & Ashelby, 2008). However, the sampling scheme reported upon in Attrill et al. (1999) was discontinued in 1992 and no records or preserved samples from other studies are known to exist from the Thames between 1992 and 2006. It is unclear, therefore, what happened during this period. One scenario is that the single individual collected in 1992 represented an unsuccessful introduction and a population failed to establish. In this instance the subsequent, abundant collections in 2006 and those from the Orwell Estuary, approximately 65km to the north, in 2001 (Ashelby et al., 2004) must have resulted from a second introduction. Another possibility is that the population survived at low abundance (a ‘sleeper’ sensu Reise et al., 2006 or a ‘minimum viable beachhead population’ sensu Hänfling et al., 2011) but didn’t become established until favourable conditions, such as increases in food availability, for example, allowed expansion. Alternatively, favourable conditions may have existed on arrival allowing the species to undergo a rapid expansion and spread beyond the River Thames to other British or European estuaries. This latter option may perhaps be discounted as it was a full six years before the next documented European records in 1998 from the Gironde Estuary, France and the downstream part of the Gent-Terneuzen Canal, Belgium near the Dutch border (Béguet et al., 2007; Boets et al.,

2011). However, it cannot be ruled out that the explanation for the lack of records from the Thames or other estuaries between 1992 and 1998 is simply a lack of suitable sampling or misidentifications in samples collected during this period.

Béguer et al. (2007) first noted specimens of *P. macrodactylus* in the Gironde Estuary in August 1998 (Figure 3A) but stated that it was in low abundance until 2002. Earlier samples examined by them from 1992 to 1997 did not contain *P. macrodactylus* providing strong evidence that the species had not arrived in the Gironde prior to 1998, or at least was a relatively recent arrival, present in sufficiently low numbers that it was not detected by their sampling methods, which were centred on the middle portion of the estuary. Likewise, initially (1998 to 2001) low numbers of *P. macrodactylus* were recorded from the Gent-Terneuzen Canal near Gent Harbour, and also only from the downstream part of the canal but it underwent a subsequent expansion phase with numbers increasing dramatically by 2003 (Boets et al., 2011).

Between 1999 and 2004 *P. macrodactylus* expanded its recorded range along Atlantic coasts (Figures 3A-B) being reported from the Guadalquivir Estuary, Spain (1999 – Cuesta et al., 2004), Westerschelde Estuary, the Netherlands. (1999 – d’Udekem d’Acoz et al., 2005), Orwell Estuary, UK (2001 – Ashelby et al., 2004), Geeste River Mouth, Germany (2004 – González-Ortegón et al., 2007) and Zeebrugge, Belgium (2004 – d’Udekem d’Acoz et al., 2005). Subsequent spread to most estuaries in France, from the Adour in the south to the Slack Estuary in the north was documented by Lavesque et al. (2010) primarily based on samples collected throughout 2006 and 2007 (Figure 3B). Its further occurrence in Belgium has been documented by d’Udekem d’Acoz et al. (2005), De Blauwe (2006), Soors et al. (2010) and Boets et al. (2011; 2012), the Netherlands by d’Udekem d’Acoz et al. (2005), Tulp (2006) and Faasse (2005), the UK by Worsfold and Ashelby (2008) and Germany by Buschbaum et al. (2012). Lavesque et al. (2010) also demonstrated that the species has not colonised all suitable estuaries in France, most notably it has not as yet been recorded from the Loire estuary despite records in the Vilaine Estuary, which joins the Loire at its mouth near the international port of St-Nazaire. Similarly, in the UK despite being present since 1992, the species has yet to be reported from the large estuaries of the Humber and Southampton Water, which also receive large amounts of shipping traffic. The reasons for these absences may be a lack of suitable sampling in these estuaries, unpublished records or a genuine absence.



**Figure 3.** North East Atlantic records of *Palaemon macrodactylus* Rathbun, 1902. A, earliest occurrence in each country or geographic area; B, introductions considered to be either primary or secondary introductions (black circles) or natural spread (open circles). The larval record off Mallorca is indicated as shaded, as no source population has been identified.

Whether the European Atlantic populations were seeded as primary introductions from Asia or secondary introductions from California is not known. However, the evidence suggests that the large European Atlantic range has been achieved through a mixture of multiple introductions (either primary or secondary) and natural spread (Figure 3B). Lavesque et al. (2010) argued for the expansion of the species in France being indicative of natural spread and passive transport of larvae by water currents (Wasson et al., 2001) and it seems reasonable to assume that this process accounts for several of the northern European records, also evidenced by the occurrence of the species in estuaries that have no commercial ports (Cuesta et al., 2004; d’Udekem d’Acoz, et al., 2005; Lavesque et al., 2010). How the species arrived in continental waters is not clear however. As the earliest known European record is from the river Thames, it can perhaps be postulated that the UK was the primary entry point to Europe. This theory may be supported by the fact that Tilbury Docks was the largest UK container port until Felixstowe Port opened in the late 1980s and Thamesport opened for operation in 1992. Working on this assumption, continental populations could have resulted either from natural spread from the UK or

a secondary introduction by short range shipping traffic. The majority of the vessels leaving from the Port of London in the Thames Estuary and from Felixstowe Port are bound for ports in mainland Europe (data from PLA, 2012; POF, 2012). Additionally, twice daily ferry traffic exists between Harwich (adjacent to Felixstowe Port) and the Hook of Holland. However, the majority of these European ports also receive shipping direct from Japan and Korea and thus a second introduction event should not be discounted.

In southern Europe, *P. macrodactylus* has been recorded from the Guadalquivir Estuary, Salado River, Guadalete Estuary and the San Pedro River, Spain (Cuesta et al., 2004) and the Guadiana Estuary, Portugal (Chícharo et al., 2009). Although, sampling programmes of the Guadalquivir Estuary were in progress in 1997 (Cuesta et al., 2004), the first records of the species in the estuary were not until January 1999 (González-Ortegón et al., 2007) when two specimens were recorded. Due to the low number of specimens recorded and the fact that it was apparently absent before this date we may hypothesise that the species arrived in southern Spain in late 1998. Despite its close proximity to the Guadalquivir, no specimens of *P. macrodactylus* were noted from the Guadiana Estuary until July 2008, even though comprehensive sampling campaigns were conducted between 1999 and 2003 (Chícharo et al., 2009). This indicates a slow rate of spread for the species in this region. It seems likely, given the lack of intermediate records between southern France (Adour Estuary; Lavesque et al., 2010) and these populations in the Gulf of Cadiz, that they represent a separate introduction event (either primary or secondary) rather than natural spread (Figure 3B). There is a paucity of suitable habitats around the Iberian Peninsular that may allow short-range, stepping stone migrations and, in particular, there are no records from the large estuaries of the Tagus (approximately 350 km around the coast from the Gulf of Cadiz, 1,100 km from the Adour) and the Mira (approximately 600 km around the coast from the Gulf of Cadiz, 800 km from the Adour), which support large populations of the native *P. longirostris* and would appear suitable habitats. Introduction to the large, international port at Sevilla in the Guadalquivir was hypothesised by Cuesta et al. (2004). As the Guadalquivir and San Francisco Bay have a number of introduced crustacean species in common (*Rhithropanopeus harrisi* (Gould, 1841), *Eriocheir sinensis* H. Milne Edwards, 1853, *Synidotea laticauda* Benedict, 1897, *Carcinus maenas* (Linnaeus, 1758)) they (Cuesta

et al. 2004) hypothesise that the Guadalquivir population results from a secondary introduction from San Francisco Bay rather than primary introduction from Asia.

#### *Black Sea – 2000s*

There are two published occurrences of the species in the Black Sea, from Constanta Harbour, Romania (Micu & Niță, 2009) and Varna Lake, Bulgaria (Raykov et al., 2010) with some of the specimens reported by Micu and Niță (2009) examined herein. The earliest occurrence in the Black Sea has been traced back to 2002 (Micu & Niță, 2009). Micu and Niță, (2009) believed it possible that the species was introduced via shipping from Rotterdam due to the continuous shipping that exists between Constanta and Rotterdam. However, it is worth noting that the occurrence in the Black Sea in 2002 pre-dates the earliest records from Rotterdam (August 2004; d’Udekem d’Acoz et al., 2005), although it seems likely that *P. macrodactylus* was present at Rotterdam long before its detection. Furthermore, Constanta Port also receives container shipping from the Far East (POC, 2012) so a direct introduction from the native range is a possibility. The Bulgarian population is likely to represent natural spread or short range vector transport from the Romanian population (Raykov et al., 2010). Sezgin et al. (2007) report on a specimen of *P. longirostris* from the southern Black Sea coast, regarding this species as non-native in the Black Sea. Several aspects of the collection data for this record are suggestive of *P. macrodactylus* and may cast doubt on this identification. The photograph included in Sezgin et al. (2007) is inconclusive, sharing a superficial similarity to both *P. longirostris* and *P. macrodactylus* but with key specific features being obscured in the photograph. A re-examination of this specimen would be desirable to confirm whether it does belong to *P. longirostris* or represents a further location for *P. macrodactylus* in the Black Sea.

#### *South West Atlantic – 2000s*

A record from Mar del Plata Harbour, Argentina (Spivak et al., 2006) represents the first published occurrence of the species in the southern Atlantic. It is one of three invasive decapod crustaceans currently established in the wild in Argentina (Tavares, 2011). This population is also unusual, in as much as the harbour

is essentially fully marine with average salinities of 32-33.7 (Schwindt et al., 2010 cited by Vasquez et al., 2012). Nevertheless the population has persisted in these conditions and the species has spread in this region with another population being found about 120 km to the south in Puerto Quequén (E. Spivak, pers. comm.). Martorelli et al. (2012) sampled additional sites between 2007 and 2011 and report the occurrence of *P. macrodactylus* in four further Argentinian locations: Río Salado flood relief channel, Tapera de López, Bahía Blanca Estuary and Río Negro Estuary, giving the species a moderately large range in Argentina (Figure 1). Further spread should be expected in South America, for example Spivak et al. (2006) predicted that the species will eventually invade the Mar Chiquita Lagoon (approximately 35 Km North of Mar del Plata) and the recent occurrence of the species in the north of Buenos Aires Province close to the border with Uruguay (Martorelli et al., 2012) suggests that it may be found in Uruguay in the near future.

#### *North West Atlantic – 2000s*

Recently, *P. macrodactylus* was recorded from the estuarine system of New York City by Warkentine and Rachlin (2010), who state that it has been present since at least 2001. Here, its presence may have been overlooked due to confusion with native *Palaemonetes* species (Warkentine & Rachlin 2010). A further study by these authors (Warkentine & Rachlin, 2012) demonstrated that the population is established and has increased in size relative to the native *Palaemonetes* species during the decade since its first discovery. In addition, Warkentine and Rachlin (2012) report an extension of the species range to the Mystic River (Connecticut). Whilst these studies represent the only published occurrences in eastern North America to date, there are also several further unpublished and unsubstantiated records from Providence River (Rhode Island), James River Estuary and York River (Virginia), Rhode River (Maryland) cited by Fofonoff et al. (2003). Warkentine and Rachlin (2010) proposed ballast water is most likely responsible for the introduction to New York but the origin remains unknown. Shipping density information (Kaluza et al., 2010) would suggest that the source of the introduction to eastern North America is likely to be either California or the newly established populations in Europe.

*Mediterranean Sea – 2005*

Torres et al. (2012) have recently provided evidence of a potential population of *P. macrodactylus* in the Mediterranean Sea. They report on the occurrence of a single larva in 2005 and a further seven larvae captured in 2010 from plankton monitoring surveys in marine waters off Mallorca, Balearic Islands. The closest known population of *P. macrodactylus* to this site is in the Gulf of Cadiz (Cuesta et al., 2004). However, Torres et al. (2012) hypothesise that given the presumed age of the larvae and water current velocities that the larvae do not originate from a distant location and it is more likely that an undetected population exists in some of the lagoons found in the Balearic Islands. A further possibility, not considered in Torres et al. (2012) is that the larvae may have been released by a passing vessel during offshore ballast water exchange. As such an exchange is now carried out by many ocean going vessels prior to entering port, and as the Balearic Islands are close to the major shipping axis from Asia to Europe, via the Suez Canal (Kaluza et al., 2010), this further option needs to be considered. Under this scenario, no undetected population responsible for larval release would need to exist in the Balearic Islands. Release of propagules from a passing vessel has already been demonstrated by Gollasch (1999) to be the initial vector for the European invasion in *Hemigrapsus takanoi* Asakura & Watanabe, 2005 (as *H. penicillatus* (De Haan, 1835)), but has received little attention as a vector mechanism.

*Possible Modes of Introduction and Spread*

Invasive species generally require a vector to reach new regions. For aquatic organisms a number of vectors and sources of introductions have been suggested (see Carlton & Ruiz, 2005 and Carlton, 2011 for reviews) including aquaculture or association with aquaculture stock, aquarium trade, use as bait, contaminated fishing gear, floating plastic debris, and use as a research organism, but introduction in association with shipping is the most frequently cited vector (e.g. Williams et al., 1982; Carlton, 1985; Briski et al., 2012). Rodríguez and Suárez (2001) summarised the most likely mechanisms of introduction in decapod crustaceans, concluding that migration through man-made navigation channels, ship transportation and aquaculture mediated introductions are the most common vectors. Recently, Briski et al. (2012)



stated that decapods present one of the highest risks for forming viable populations following transport in ballast water.

Several invasive species, in particular gastropod molluscs, boring polychaetes and seaweeds, have been introduced to new areas in association with the transportation of oysters (Carlton, 1979). Transport within mesh bags used for transporting oysters has been suggested as a possible mode of spread for *Hemigrapsus* spp. within Europe (Minchin, 2007). Some European records of *P. macrodactylus* are indeed from areas away from large ports and in areas that are associated with Pacific oyster (*Crassostrea gigas* (Thunberg, 1793)) cultivation such as the Oosterschelde (Smaal et al., 2009) and Arcachon Bay (Grizel & Héral, 1991), which may lead to the suspicion of oyster transport as a vector. However, oysters are usually transported damp, with limited amounts of water trapped in pockets of the empty valves used for cultch (Carlton, 1979) and it is unlikely that *P. macrodactylus* could survive emersion for prolonged periods, or be transported in sufficient numbers in the limited water available, so it seems unlikely that these would provide a suitable vector in this case.

In addition to shellfish, introductions in association with finfish have also been reported. Two species of *Palaemon*, *P. adspersus* Rathke, 1837 and *P. elegans* Rathke, 1837, were transported to the Caspian Sea and Aral Sea; their introduction to these areas in the early 1930s is believed to be coincidental with the introduction of mullet from the Black Sea in the early 1930s (Zenkevich, 1963; Grigorovich et al., 2002).

Given the disjunct global distribution of the species and that most new records of *Palaemon macrodactylus* are from the vicinity of large, international harbours (e.g. Ashelby et al., 2004; Cuesta et al., 2004; d'Udekem d'Acoz et al., 2005; Spivak et al., 2006; Béguer et al., 2007; González-Ortegón et al., 2007; Micu & Niță, 2009; Warkentine & Rachlin, 2010) it is most likely that introduction to these regions is shipping mediated, with transport in ballast water or as a fouling organism within the sea water intakes or sea chests of vessels being the most likely candidates. Newman (1963) presented a convincing argument that the introduction of *Palaemon macrodactylus* to San Francisco Bay was coincidental with an increase in shipping to the region from Japan and Korea following the Korean War with the species most likely travelling in the cooling water systems of ships. The current distribution of *P. macrodactylus* closely matches maps of global shipping density (Kaluza et al., 2010) and known ballast water mediated introductions (Drake & Lodge, 2004). Whilst it is

true that these are the most likely vectors, most published studies on ballast water only report ‘unidentified decapod larvae’ (Briski et al., 2012) and no documented occurrences of larvae of *P. macrodactylus* being found in ballast water or adults being reported from ship-fouling communities exist. Once established in a region natural spread via larval dispersal, short-range migrations (Lavesque et al., 2010) or infra-regional shipping is probable, as appears to be the case in Europe. Carlton (1985) and Williams (1997) suggest that the spread of *P. macrodactylus* along the coast of California was accelerated by the species’ use as bait but this has not been reported in other regions.

#### *Synopsis of Biological Data on Palaemon macrodactylus*

##### *Physiological and Environmental Tolerances*

*Palaemon macrodactylus* has broad environmental tolerances. In particular, it tolerates wide ranges of temperature and salinity and is particularly tolerant of hypoxic conditions (González-Ortegón et al., 2006). It is a strong osmoregulator over the salinity range of 2-150‰ sea water, and is known to inhabit a wide range of salinities in San Francisco Bay (Born, 1968), where it is not uncommon to capture *P. macrodactylus* in fresh or nearly fresh water (Siegfried, 1980). The upstream limit of its range in California has been noted as 1PSU, the downstream limit being set by prey availability (Siegfried, 1980). More recent records from Gent Harbour, Belgium (Boets et al., 2012) have also been from apparently freshwater, whereas the population in Mar Del Plata Harbour, Argentina is established in fully marine conditions (Vázquez et al., 2012). González-Ortegón et al. (2006) demonstrated that the centre of mass of the population with respect to distance from the river mouth and salinity was related to temperature with *P. macrodactylus* occupying a wider range at lower temperatures. The isosmotic point for *P. macrodactylus* is 584 mmol kg<sup>-1</sup> at 20°C (González-Ortegón et al., 2006) and it effectively osmoregulates over much of its salinity range.

*Life History and Growth*

The life history characteristics show some variation between native and non-native populations of the species. Omori and Chida (1988a), working on a population in Japan, described the breeding season of *P. macrodactylus* as being mid-April to early October. In California, ovigerous females are found mainly from May to August (Siegfried, 1980); juveniles being recruited to the benthos after May (Siegfried, 1980; 1982), whereas in Argentina the breeding season is during the austral summer, October to March (Vazquez et al., 2012). Siegfried (1980) noted that photoperiod is an important parameter in controlling spawning. Second-year females carry eggs earlier than first-year females (Omori & Chida, 1988a). Most 0-1 year old females produce less than 1000 eggs at temperatures of between 15°C and 27°C whilst older females produce 500-2,800 eggs at similar temperatures (Omori & Chida, 1988a). Brood sizes of between 100 and 2000 have been noted for Californian specimens of the species and females may carry a second brood in their ovaries before the first brood is released (Siegfried, 1980). Each age group produces at least two cohorts per year, with five to nine being possible under controlled laboratory conditions entailing a raised temperature and hence an extended breeding season (Omori & Chida, 1988b). Higher salinities may also extend the breeding season of *P. macrodactylus* (Little, 1969).

In *Palaemon macrodactylus*, growth rate is very high in the first year and there is a spurt of growth just before spawning; little growth occurs after spawning until the following year. Sexual characteristics are noted on individuals 20 mm in length (Siegfried, 1980) and females grow faster than, and are larger than, males (Omori & Chida, 1988a). Life spans of two to three years have been recorded for individuals of *P. macrodactylus* in Japan (Omori & Chida, 1988a, c). Recently, Vázquez et al. (2012) reported that the population of *P. macrodactylus* in Mar del Plata harbour, Argentina had shorter life spans and were generally smaller than those in the native range, possibly linked to the stresses of surviving in high salinity rather than estuarine conditions.

### *Diet*

*Palaemon macrodactylus* is omnivorous but the greater proportion of the diet is made up of animals, with Sitts and Knight (1979) recording between 75 and 93% of gut content consisting of animal fragments. It predares on mysids, copepods, amphipods, barnacles, polychaetes, small bivalves, fish larvae (Sitts & Knight, 1979) and insect larvae (pers. obs.). There is also evidence of cannibalism when kept in crowded laboratory conditions (Newman, 1963). Whether this also occurs in nature or is extended to feeding on other carideans is not known.

### *Factors Favouring the Successful Introduction of Palaemon macrodactylus*

To date, three other species of *Palaemon* have been recorded as non-native in various areas. *Palaemon longirostris* was reported as non-native in the southern Black Sea (Sezgin et al., 2007 – but see comment above in the discussion about Black Sea *P. macrodactylus* records). Both *P. adspersus* and *P. elegans* have been recorded from the Caspian Sea and Aral Sea. *Palaemon elegans* has also been reported from Lake Abu-Dibic in Iraq (Holthuis & Hassan, 1975) and, most recently, from Massachusetts, U.S.A. in 2010 (J. Carlton, pers. comm.). *Palaemon elegans* has also recently colonised a large part of the Baltic Sea, where it has been present since at least 2000 (Janas et al., 2004; Grabowski, 2006; Kotta & Kuprijanov, 2012). Although natural spread to the Baltic from North Sea coasts was considered a possibility by Grabowski (2006), Köhn and Gosselck (1989) who reported the presence of the species in Wismarer Bucht, suggested that its sporadic occurrence resulted from larvae arriving in ballast water. More recently, Reuschel et al. (2010) demonstrated that Baltic *P. elegans* belonged to a genetic haplogroup that was otherwise only found in the Mediterranean and Black Sea strongly suggesting that the occurrence of this species in the Baltic is indeed human mediated. However, *P. adspersus*, *P. elegans* (and possibly *P. longirostris*) have not achieved the same global spread as *P. macrodactylus* posing the question as to why *P. macrodactylus* has achieved a greater number of introductions than other *Palaemon* spp. One possibility may simply be that other species of *Palaemon* have been introduced to the same extent but have remained undetected in their new environments. Indeed, De Grave and Mann (2012) speculated that a population of another palaemonid prawn,

*Exopalaemon modestus* (Heller, 1862), in Kazakhstan may have gone undetected for more than 50 years. A more likely explanation is that there will be certain facets of the species' ecology or biology that specifically favour the introduction of *P. macrodactylus* over other species.

Hänfling et al. (2011) summarised characteristics that may provide advantages to invasive crustaceans and concluded that, whilst no individual trait seems to have a greater influence, certain characteristics such as eurytolerance, omnivory and certain r-selected life-history traits such as high fecundity, long reproductive season, short generation time and ability to disperse offspring resulted in a high probability of alien crustacean species becoming invasive. However, Miller and Ruiz (2009) warn against trying to explain the success of an invasive species through analysis of its biological characteristics alone. They suggest that it is necessary to consider the interactions between source regions, recipient regions, and transfer mechanisms (vectors) but state that successful introductions will also have a temporal aspect.

In order to be introduced to a new region a species must successfully navigate a series of filters (Kolar & Lodge, 2001; Sakai et al., 2001; Alonso & Castro-Díez, 2008). These filters are: overcoming the physical barriers between native and recipient environments (transport), survival, growth and reproduction under the new environmental conditions (establishment), and high rate of population growth (spread). The challenges of each of these filters are different and thus the traits required to overcome these challenges are also different. No single biological trait will explain or lead to a successful introduction. Only organisms that have a combination of traits that allow them to overcome, in the balance of probability, the challenges of each of the filters will successfully establish in new regions. Additionally, the relative importance of these required characteristics may vary among different invasion events of the same species as well as among stages of the invasion process (Hänfling et al., 2011).

The successful introduction of *P. macrodactylus*, as with most organisms, will thus rely on the combination of, and interaction between, a number of biotic and abiotic traits and chance factors.

### *Biotic Factors*

Many biological aspects of *P. macrodactylus* are not unique to this species, being shared with other *Palaemon* species, but the combination of these factors may provide a clue as to why it has been so successful at colonising new areas. Some possible biological traits that may aid the species at each stage of invasion are discussed here.

In order to successfully navigate the first filter (transport) there must be a vector for transport and there must be a way for an organism to exploit this. In the case of *P. macrodactylus* this vector is assumed to be ballast water or fouling within the sea water system of ships. The ability to apply pressure on the recipient environment either through weight of numbers or frequency of introductions has been cited as a key factor in explaining the success of many introduced species (Simberloff, 2009). The probability of successful invasion by *P. macrodactylus* therefore must rely on numbers and/or frequency of introduced propagules. Adult decapods have been reported from ballast tanks (Briski et al., 2012) but it is not known whether they can be entrained into and discharged from ballast water systems in viable condition. On the assumption that an adult could pass through the system undamaged, whether it can establish a population partly depends on its reproductive strategy. In parthenogenic organisms, self-sustaining populations can result from the introduction of a single individual (Scholtz et al., 2003; Alonso & Castro-Díez, 2008), albeit resulting in low genetic diversity. However, for organisms requiring sexual reproduction, either at least one adult of each sex must be entrained or fertilisation must have occurred prior to entrainment. Briski et al. (2012) report an ovigerous female of the crab, *R. harrisi* from ballast tanks, demonstrating that this latter scenario can occur. As previously mentioned, an ovigerous female *P. macrodactylus* can carry up to 2000 eggs, which, if all released into the recipient environment, would result in significant propagule pressure. Repeated introductions through ballast are, however, likely to be common place with various ships following the same shipping routes, with potentially the same ‘biological cargo’ in their ballast tanks. Evidence of this may be found in the study by Briski et al. (2012) who record the presence of an adult *Carcinus maenas* in ballast tanks of ships arriving in Canada, where the species has already colonised. Not only does this indicate repeated invasions are likely to

occur but it also indicates that gene-flow is likely to be maintained, overcoming potential genetic bottlenecks.

Whilst the evidence of Briski et al. (2012) demonstrates that benthic adult decapods can be entrained, ballast water intakes are usually situated on the hull of the vessel several metres below the water line (Gramling, 2000) but not near the seabed, reducing the likelihood of entraining primarily benthic organisms. Rather it is pelagic organisms and planktonic larvae occurring in the water column that are likely to be entrained. These are also more likely to be entrained in high abundance. Given that propagule pressure is an important factor in determining the success of an invasion (Simberloff, 2009) and the comparatively low likelihood of entraining adults, transport of *P. macrodactylus* most likely occurs as larvae.

Between 2002 and 2004, shortly after the earliest records of *P. macrodactylus* from the vicinity of Felixstowe Port, which is the largest commercial port in the UK handling 40% (over 3.4 million TEUs per year; POF, 2012) of Britain's containerised trade, a two year study into the zooplankton composition of the area was conducted (Dyson, 2005). During this study, *Palaemon macrodactylus* larvae reached a maximum density of 210 per m<sup>3</sup>, were frequently in densities in excess of 100 per m<sup>3</sup>, and were present between May and October with low numbers also being present in December (Dyson, 2005). The only other decapods to achieve higher larval densities in that study were *Crangon crangon* (Linnaeus, 1758) and *Carcinus maenas*, the latter species has likewise achieved a near global distribution (Carlton & Cohen, 2003). With even moderate sized vessels having ballast tanks with a capacity of over 500 m<sup>3</sup> (Ruiz et al., 2005), this suggests that potentially tens of thousands of larvae of *P. macrodactylus* could be transported by a single vessel. The larvae of *P. macrodactylus* are photopositive (Little, 1969) and would therefore be susceptible to being entrained into ballast water during the day. At night they may be attracted to harbour lights and hence towards ships taking on ballast. Furthermore, the adults are present in the water column at night (Siegfried, 1982) perhaps putting them at risk of entrainment themselves. Once entrained the propagules (larvae or adult) must be able to survive the often harsh conditions of ballast tanks (Briski et al., 2012). Conditions within the tank are subject to large fluctuations in temperature, salinity, dissolved oxygen and nutrition. Many of the broad environmental tolerances detailed above such as euryhalinity and tolerance to hypoxia would aid the survival of adult *P. macrodactylus* in ballast tanks. In particular the tolerance of *P. macrodactylus* to

hypoxic conditions (González-Ortegón et al., 2006) may provide it with an advantage during transport in ballast water. Reid et al. (2007) concluded that dissolved oxygen decreased by 90% over a 10 day journey at temperatures of 22-28°C although no reduction in dissolved oxygen occurred at 3-5°C. *Palaemon macrodactylus* is ideally suited to cope with this reduction in dissolved oxygen and may, therefore, have an increased likelihood of survival over species with lower tolerances to hypoxic conditions. However, many transoceanic journeys exceed 10 days transit time and the further decrease in dissolved oxygen and whether *P. macrodactylus* could tolerate these hypoxic conditions for such prolonged periods are not known. In spite of the broad tolerances shown by adults, as it is considered that larval transport is more likely in *P. macrodactylus*, the environmental tolerances of the larval stages would be more important in determining survival during transport and the success of overcoming the first filter. Although Little (1969) indicates that *P. macrodactylus* larvae are robust, their environmental tolerances are not known but broad tolerances may also be expected. Studies into the tolerances of larvae to fluctuations in salinity, hypoxia, temperature and other environmental conditions may therefore be highly rewarding and make progress towards explaining how *P. macrodactylus* overcomes the transport stage of invasion.

Following delivery to the recipient environment, initial survival requires that the organism arrives at a suitable habitat (directly or indirectly) and that it can face the immediate proximate environmental challenges. As ports are often built in large estuaries to take advantage of the natural shelter they provide, it is likely that any individuals of *P. macrodactylus* incorporated into ballast or a fouling community would be delivered to a favourable habitat. Again, the wide environmental tolerances of *P. macrodactylus* detailed above increase the likelihood that the recipient habitat would at least be tolerable.

Once delivered to its new environment, ultimate biotic factors then need to favour the successful colonisation by *P. macrodactylus* including competition, predation, fecundity, longevity, growth rate and diet.

In each region to which *P. macrodactylus* has been introduced, it has successfully spread to a greater or lesser degree. This is likely to have been achieved through a combination of the species' dispersal phase and its' ability to utilise short-range vector transport. Both these scenarios were suggested by Lavesque et al. (2010) for the spread of the species along the west coast of France. The planktonic larval



phase is between 12 and 18 days (Little, 1969) and thus passive transport via favourable water currents is possible and is probably the main method by which the species spreads on a regional scale.

#### *Abiotic Factors*

The success or failure of an introduction relies as much on the vector, source region and recipient region as it does the biology of the species in question (Miller & Ruiz, 2009). A number of features of the recipient environment may favour the successful introduction by *P. macrodactylus*. As previously mentioned, ports and harbours are often built in estuaries and thus within, or close to, *P. macrodactylus*' preferred salinity. Harbours are often characterised by low biological diversity and an availability of vacant or underexploited niches (Eno et al., 1997; Nehring, 2006). The routine dredging that takes place in harbours may further serve to open up niches by removing native communities, altering sediment dynamics and mobilising pollutants. In this way, *P. macrodactylus* may function as an opportunistic species exploiting these disturbed niches before they are re-colonised by the native fauna. Siegfried (1980) regarded *P. macrodactylus* as tolerant to pollution and it may therefore also be able to survive in polluted regions of the harbours that are avoided by incumbent native species. Indeed, the first record of the species from the Thames Estuary was coincidental with a drought period between 1989 and 1992 which led to both increased salinity and increased concentrations of some heavy metals, in particular lead (Power et al., 1999).

There is a high likelihood that the successful introduction of *P. macrodactylus* to a new region also has a temporal aspect (Miller & Ruiz, 2009). Seasonality will effect the invasibility of a region as well as the supply of propagules (Miller & Ruiz, 2009) leading to a window of invasion opportunity (Carton, 1996). The entrainment of larvae would only occur during the breeding season whilst their survival during transport or on arrival in the recipient environment may also be seasonally controlled.

#### *Stochastic Factors*

Many of the features identified above may have favoured the first colonisation event to California but a further possible reason that *P. macrodactylus* has been so

widely spread is that this initial successful colonisation event occurred. With every successful introduction a new source population is established to potentially seed further introductions. By first establishing in the NE Pacific it then had two potential source populations to spread to other areas and so on. Each new population may put other regions within striking distance that would have perhaps been out of reach of a direct introduction from Asia due to transit times or an absence of direct shipping. However, conflicting with this, according to Kaluza et al. (2010) Asian ports are amongst the most highly connected and data held by the World Shipping Council (WSC, 2012), suggests that 13 of the top 20 busiest trade routes for container shipping worldwide (including routes to Europe and the U.S.A.), originate from Asian ports suggesting that multiple introductions from the native range may actually be more likely.

At present it is not possible to definitively conclude whether multiple introductions from Asia, secondary introductions from non-native populations or a combination of both methods have facilitated the global spread of the species. However, based on the balance of evidence it is possible to speculate that primary introductions account for the occurrence in western North America, Australia and Northern Europe whilst secondary introductions are responsible for the eastern North America, Black Sea and possibly Spanish populations. Short-scale secondary introductions are also likely to have aided the species' spread in Europe and western North America. The origin of the Argentinean population is unclear and may have originated either from Asia or another invaded region.

#### *Potential Impacts*

All organisms introduced outside of their native range will exert some influence on recipient communities. The scale and nature of this influence may be hard to objectively quantify as impacts are scale-dependent, vary between geographical regions (Carlton & Cohen, 2003), depend on the phase of invasion, the recipient biota and current habitat conditions (Reise et al., 2006). Whilst many introduced species have, in the past, proven to be damaging to indigenous biota, this is not always the case and effects witnessed in one area may not be mirrored in other regions and care should be taken not to assume that there will be a negative impact without evidence (Reise et al., 2006). Simberloff (2010) notes that there may be a

significant time lag between introduction and any witnessed impacts. Thus, many introduced species are ‘biological time bombs’, being innocuous for years in their introduced environment before having major impacts when conditions are favourable (Simberloff, 2010).

Few data exist on competitive interactions of *Palaemon macrodactylus* in either its native or introduced ranges. The available data suggest its’ impacts may not be as severe as those reported for some other species but that is not to say it is totally benign. As previously mentioned, one possible reason that *P. macrodactylus* has successfully invaded and established in new areas is that it is able to use niches not exploited by native species. By exploiting these vacant or under-used niches, *P. macrodactylus* may be able to minimise or avoid competition with native species. Béguer et al. (2011) indicated that *P. macrodactylus* exploits niches in the Gironde Estuary, France that are currently under-used by the native *Palaemon longirostris* thus reducing competition. However, conflicting with this, a later study on the population in the Gironde (Béguer et al., 2012), cited competition with *P. macrodactylus* as a possible contributing (but not necessarily causative) factor in the decrease in abundance of *P. longirostris*. In contrast to the situation in Europe, in San Francisco Bay there is a paucity of native palaemonid taxa, with the shrimp fauna being dominated by crangonids. Crangonid shrimp occupy a different ecological niche than palaemonid shrimp reducing the likelihood of potentially damaging effects from the introduction of *P. macrodactylus* (Newman, 1963; Carlton, 1979). However, Sitts and Knight (1979) and Siegfried (1982) found that there was dietary overlap, with size-related resource partitioning, between this species and the indigenous *Crangon franciscorum* Stimpson, 1857, in California and González-Ortegón et al, (2010) also showed dietary overlap with *P. longirostris* in Spain. Ricketts et al. (1968) observed that *P. macrodactylus* had eclipsed native (American) *Crangon* spp. in terms of numerical abundance since its introduction and Siegfried (1980) felt that careful management of water projects may be necessary to protect the native shrimp (*C. franciscorum*) in the Sacramento/San Joaquin Delta. Importantly, though, neither of these studies demonstrated detrimental effects on or a decrease in the abundance of *Crangon* spp.

Some potential impacts of the introduction of *P. macrodactylus* to Europe were discussed by Ashelby et al. (2004) and by González-Ortegón et al. (2005) and include competition and conflict with native shrimp species (dietary, predatory,

habitat), displacement of native species and the potential introduction of new pathogens. Indeed, González-Ortegón et al. (2010) demonstrated high trophic overlap between *P. macrodactylus* and *P. longirostris* in the Guadalquivir Estuary, Spain suggesting that they do compete for certain resources. The actual impact of this competition on the native species has not been quantified but does not appear to be significant under current conditions. However, González-Ortegón et al. (2010) believed that if the estuary became more hypoxic in the future, *P. macrodactylus* would have a competitive advantage and may increase its range and abundance at the expense of *P. longirostris*.

The potential introduction of a species' natural pathogens should always be considered when discussing the potential impacts of non-native species. For example, the introduction, spread and effects of crayfish plague in Europe have been well documented (e.g. Schrimpf et al., 2012 and references therein). However, in many cases the natural pathogens of the species or those already present in the recipient environment may not be known and so these may be difficult to quantify. As with many decapods, the eggs of *P. macrodactylus* are susceptible to infection by the fungus *Lagenidium callinectes* Couch, 1942 (see Fisher, 1983b) which may result in the death of embryos. However, *P. macrodactylus* has a symbiotic bacterium, *Alteromonas* sp., which protects its eggs from fungal attack (Fisher 1983a, b; Gil-Turnes et al., 1989). It is unknown how many other species of *Palaemon* have similar bacteria and no studies have been undertaken to investigate whether the specific strain of *Alteromonas* has been transferred to other species in recipient regions. Martorelli et al. (2012) report high instances of infection of *P. macrodactylus* by white spot syndrome virus (WSSV) in Argentina and Martorelli et al. (2010) speculated that WSSV could have been introduced to Argentina by WSSV-infected *P. macrodactylus*, although several other potential sources of the virus are also mentioned. Martorelli et al. (2012) also reported that, since its introduction, *P. macrodactylus* has acquired a role in being a second intermediate host in the life cycle of the helminth parasite *Odhneria* sp. Whilst spread of these parasites and pathogens to native species has not yet been documented, the situation should be closely monitored.

Other potential impacts discussed for non-native species (Eno et al., 1997) include the alteration of trophic links, habitat alteration, threats to native or endangered species, potential hybridisation or dilution of the gene pool. In addition,

some potential positive effects have been suggested for *P. macrodactylus* including the provision of an additional food and fisheries resource or use as a potential test organism (Ashelby et al., 2004).

#### *Potential range and prediction of future spread*

Successful introductions are generally from similar latitudes (Eno et al., 1997) and, as with many species, the potential range of *P. macrodactylus* is most likely to be limited by temperature. The species has already been recorded in many suitable regions and it is highly likely that *P. macrodactylus* will be introduced to (or is already present but undetected), other regions with suitable temperature regimes through a suitable vector. Its current distribution closely matches the regions indicated as of highest likelihood of ballast water invasions by Drake and Lodge (2004). In regions to which *P. macrodactylus* has been introduced it is likely that, in time, it will colonise all suitable habitats either through natural spread or infra-regional shipping. In north-east Europe, González-Ortegón et al. (2007) predicted the occurrence of the species in the Baltic Sea via spread through the Kiel Canal, although it may also spread via shipping to there, as has been suggested for the introduction of *P. elegans* to the Baltic (Reuschel et al., 2010). The invasion of the Mediterranean may already have begun based on the larval evidence presented in Torres et al. (2012). Given a suitable vector, it could further spread to suitable habitats in Southern Norway and north-west Africa. Further spread along both coasts of North America and the Atlantic coast of South America should be expected and further introductions to southern Australia and South Africa are probable. Longer-term, the continued effects of climate change (Occhipinti-Ambrogi, 2007) may put other regions, currently outside of *P. macrodactylus*' tolerated temperature range, at risk of invasion. Spread between disparate areas is most likely to occur via shipping and its occurrence in large harbours throughout its native and introduced range increases the opportunities and likely destinations. Laboratory studies into tolerance limits for many environmental parameters are lacking and would provide useful insights into potential areas at risk of invasion by *P. macrodactylus*.

## Conclusions

*Palaemon macrodactylus*, a large edible shrimp of north-east Asian origin, has been transported to six regions outside of its native range in just over half a century. It is thought transport as larvae in association with shipping is the most likely vector for *P. macrodactylus*' global spread. It is currently known from western North America (British Columbia south to California), eastern North America (New York and Connecticut), Argentina, northwest Europe (Germany southwards to southern France, the UK and southern Spain), the Black Sea (Romania and Bulgaria) and possibly Australia (N.S.W.). In the absence of recent, verified records from Australia, its continued presence cannot be confirmed but the south-west, south and south-east coasts of Australia are liable to re-invasion if the original population has not persisted. Other regions that have so far escaped invasion by *P. macrodactylus*, such as South Africa, are at risk of colonization and the species' spread and effects on native biota outside of its natural range should be closely monitored.

Once established in a region, *P. macrodactylus* apparently undergoes rapid expansion and achieves broad geographic ranges in comparatively short time frames. It is likely that this regional spread is achieved through a combination of natural spread and short-range vector transport but some records are suggestive of further primary introductions. Primary introductions from Asia are thought most likely for western North America, Australia and Europe. The Black Sea population and, possibly the eastern North American populations, are hypothesized to have originated as secondary introductions from Europe whilst the southern Spanish population may be indicative of a secondary introduction to Europe from western North America. The origin of the Argentinean population is unclear and may have originated either from Asia or another invaded region. A pattern that has been repeated in most regions has been that following arrival, *P. macrodactylus* appears to survive as a small population for a few years before numbers increase dramatically and the species begins short-range spread.

A number of aspects of the biology of *P. macrodactylus* may contribute to its success in distributing globally, but most of these traits are applicable to other species of *Palaemon*. It is therefore unclear why *P. macrodactylus* has achieved global spread where other species have not, but studies into the environmental tolerance of the larvae may further help explain how it is able to overcome the challenges of

transport in ballast water and may provide a clue as to why it has become such a successful invader.

### Acknowledgements

R. Buckworth is thanked for providing a copy of his thesis on *Palaemon macrodactylus* in Australia; P. Boets provided information on his early record of *P. macrodactylus* from Gent Harbour; T. Komai and J.N. Kim provided valuable information on the distribution of *P. macrodactylus* in its native range whilst J. Carlton and J. Chapman are thanked for sharing their observations of *P. macrodactylus* in western North America. C. Fransen kindly searched through the Holthuis correspondence archive on our behalf. The following people are kindly acknowledged for providing material, further information and/or literature not available to us: S. Keable, G. Dally, K. van Dorp, C. Fransen, T.-Y. Chan, E. Spivak, L. Harris, J. Taylor, P. Davie, J. Short and G. Poore. Thomson Unicomarine partially supported the work of the first author and much of the initial work for this study was conducted during the compilation of a datasheet on *Palaemon macrodactylus* for the CABI Invasive Species Compendium (<http://www.cabi.org/isc/>) by the first author.

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## Appendix

Material examined during this study (ovigerous females are indicated as ov., unsexed specimens as spec.). Unless otherwise indicated all material listed is identified as *Palaemon macrodactylus* Rathbun, 1902.

### Native Range

Japan:

Mano Bay, Sado Island, Japanese coast of the Sea of Japan; 1 ov. ♀; 28 July 1978 (OUMNH.ZC.2003-10-12). Kaneda Beach, Obitsu River Estuary, Kisarazu, Chiba Pref; 11 ♂♂, 25 ♀♀; 28 October 2011 (OUMNH.ZC.2011-11-27). Mouth of the river at Toba, Kii Peninsula, Mie Prefecture, Honshu; 1 ♀, 4 ov. ♀♀; 7 May 1979 (RMNH.CRUS.D.32098).

Republic of Korea:

Fusan; 1 ♂, 1 ov. ♀, 2 spec.; 1885 (RMNH.CRUS.D.8985). Yangpo, Gyeongbuk; 1 ♂, 1 ♀; 15 April 2002 (OUMNH.ZC.2012-01-45).

### Northeast Pacific

California, U.S.A.:

San Joaquin River, Twitchell Island; 2 ♂♂, 2 ♀♀; August 1962 (RMNH.CRUS.D.18942). Palo Alto Yacht Harbour, South San Francisco Bay; 21 ♂♂, 28 ♀♀; 7 January 1962 (RMNH.CRUS.D.18938). Berkeley Aquatic Park, Berkeley; 16 ♂♂, 4 ♀♀, 7 ov. ♀♀; July 1961 (RMNH.CRUS.D.18939)

### Australia

New South Wales:

Vales Point power station, Lake Macquarie; 1 ♂, 3 ♀♀, 1 ov. ♀; January 1978 (AM P.27411). Hunter River, Newcastle; 1 ov. ♀; 1967 (AM P.16203)

Northern Territory:

Mouth of the Blackmore River, Channel Island, Darwin; 1 ♂; 12 June 1991 (NTM Cr.008363) (material identified as *P. macrodactylus* in Bruce & Coombes, 1997, re-identified herein as a juvenile *Macrobrachium* sp.). Near Bridge Channel Island,

Darwin; 2 ♂♂, 2 ♀♀, 1 ov. ♀; 21 November 1991 (NTM Cr.009987) (material identified as *P. macrodactylus* in Bruce & Coombes, 1997, re-identified herein as a juvenile *Macrobrachium* sp.)

### **Tropical eastern Pacific**

Taiwan:

Donggang, Pingtung County; aquaculture pond; 9 ♂♂; 7 June 1984; NTOU (material identified as *P. macrodactylus* in Chan & Yu, 1985, re-identified herein as *P. serrifer*).

Donggang, Pingtung County; aquaculture ponds; 52 ♂♂, 43 ♀♀, 24 ov. ♀♀; 28 July 2009 (OUMNH.ZC.2010-02-0077); *Palaemon serrifer*.

### **Northeast Atlantic**

United Kingdom:

Tilbury Power Station, Thames; 23 ♂♂, 126 ♀♀; 24 January 2007 (NHM 2008.862-871). Tilbury Power Station, Thames; 26 ♂♂, 76 ♀♀; 25 October 2006 (NMSZ.2008.030). Greenwich, Thames; 8 spec.; 19 September 2005 (OUMNH.ZC.2006-01-0040). West Thurrock Power Station, Thames; 1 spec.; 13 November 1992 (OUMNH.ZC.2006-01-0041). River Orwell, Suffolk; 6 spec.; 14 February 2002 (OUMNH.ZC.2005-02-0001).

France:

Gironde Estuary; 4 ♀, 1 ov. ♀; 23 May 2007 (OUMNH.ZC.2007-10-0002).

Spain:

Guadalquivir Estuary; 8 ♂♂, 5 ♀♀, 1 spec.; 13 November 2004 (OUMNH.ZC.2005-03-0002). Guadalquivir Estuary; 1 ♂, 1 ov. ♀; April 2003 (RMNH.CRUS.D.50429).

The Netherlands:

Hansweert, Zuid-Beveland; 3 ♂♂, 2 ov. ♀♀; 30 July 2004 (RMNH.CRUS.D.51414).

### **Southeast Atlantic**

Argentina:

Mar del Plata Harbour; 6 ♂♂, 10 ♀♀; April 2012 (OUMNH.ZC.2012-01-0069).

**Black Sea**

Romania:

Constanta Harbour, downstream of the Danube-Black Sea Canal sluice gates; 3 ov.

♀♀; 5 September 2009 (RMNH.CRUS.D.53190).





**Diet analysis indicates seasonal fluctuation in trophic overlap and separation between a native and an introduced shrimp species (Decapoda: Palaemonidae) in the Tidal River Thames**

**Abstract**

In lower salinity regions of the Tidal River Thames the two most common shrimp species are *Palaemon longirostris* and *P. macrodactylus*. This latter species is a non-native species in Europe and its competitive interactions with native species have not yet been fully explored. In this study the diet of these species was investigated through stomach content analysis. Samples from both summer and winter were analysed to investigate any potential seasonal variations. The data show that both species are largely carnivorous with corophiid amphipods forming a large proportion of the diets of both species, whilst mysids, nereids and plant material were also commonly consumed. Chironomid larvae were consumed in large numbers by both species in summer but were not present in the diet during winter. Vacuity coefficients were higher for both species in winter than in summer indicating a lower rate of feeding in the winter. The data also show that whilst there is a high dietary overlap in winter the diets did not overlap to the same degree in the summer. This suggests that the two species are competing for food on a seasonal basis. The observed difference may be partly attributed to the absence of chironomid larvae, and generally reduced prey availability, in the winter. If summer prey also become limited then there would be potential for increased competition between these two species for food. This may lead to *P. macrodactylus* having an adverse effect on the native *P. longirostris*. This result also indicates that an introduction event of *P. macrodactylus* in the summer, when there is less competition for food, may perhaps be more likely to lead to a successful colonisation than one in the winter.

**Introduction**

The oriental prawn *Palaemon macrodactylus* Rathbun, 1902 has recently been introduced to several worldwide locations. A summary of the invasive history, biological traits and potential impacts of the species was recently presented by

Ashelby et al. (2013). This review identified a shortfall in the knowledge as to exactly how the species interacts with native species in its new environment. Very few introduced species are truly benign and most species newly introduced to an area will compete with incumbent species for resources in some form, particularly with closely related species or those that share similar lifestyles, behaviour and environmental tolerances. How native and introduced species interact and the degree of competition is key to understanding the potential impacts of an introduction. A crucial resource for which introduced and native species may compete is for food. Indeed, being omnivorous or a generalist feeder is a trait that may favour the establishment of a species following introduction to a new region (Hänfling et al., 2011).

In Europe the first record of *P. macrodactylus* has been traced back to 1992 from the River Thames, UK (Worsfold & Ashelby, 2008). Here it coexists with the native *Palaemon longirostris* H. Milne Edwards, 1837, a species that is reported to have some conservation importance (Chadd & Extence, 2004). Since then several studies have reported the co-occurrence of these two species in estuaries throughout north-western Europe (reviewed by Ashelby et al., 2013). The association between these species is relatively recent and few quantitative data exist as to the interaction between these species in the River Thames and particularly whether there is competition for food.

Previous studies on the diet of *Palaemon macrodactylus* in San Francisco Bay (Sitts & Knight, 1979; Siegfried, 1982) and in Spain (González-Ortegón et al., 2010) have shown that the species is predominantly carnivorous with the majority of its diet comprising crustacean prey. There is also evidence of cannibalism when kept in crowded laboratory conditions (Newman, 1963). This predominantly carnivorous diet is in general agreement with the diet reported for other *Palaemon* species (Forster, 1951a, b; Guerao, 1994, 1995; Janas & Barańska, 2008) and it is therefore expected that there will be a high degree of dietary overlap with other *Palaemon* species in regions to which it has been introduced. Indeed, González-Ortegón et al. (2010) demonstrated trophic overlap between *P. macrodactylus* and *P. longirostris* in the Guadalquivir Estuary, Spain. In this study we investigate the hypothesis that *Palaemon macrodactylus* will also compete for food with *P. longirostris* in the Thames Estuary.

## Material and Methods

### *Sample collection*

The samples of *Palaemon* used in this study were collected as part of a long term study by the Zoological Society of London (ZSL). The primary aim of the study was to provide data on fish populations in the Tidal River Thames and the collection of decapods was an incidental by-catch to this study. Samples were taken at monthly intervals from the cooling water intake filter screens of Tilbury Power Station, Essex UK (51°27'6.5"N 0°23'19.0"E) using the methods established by Attrill et al. (1999). Samples were obtained using a continuous suction effort of 30 minutes. Preliminary sorting of the samples was conducted in the field by ZSL with decapods being transferred straight to 75% ethanol and sent to the Oxford University Museum of Natural History (OUMNH).

### *Determination of species and gender*

Specimens were identified using the combination of characters given in recent keys to the Palaemonidae of North-West Europe (Ashelby et al., 2004; d'Udekem d'Acoz et al., 2005; Gonzalez-Ortegon & Cuesta, 2006) and sex was determined based on the presence (males) or absence (females) of an appendix masculina on the endopod of the second pleopod.

### *Stomach content analysis*

Samples collected between December 2006 and February 2007 (winter samples) and between June and September 2007 (summer samples) were selected to provide seasonal comparison of diets.

Following identification and sexing the shrimp were dissected and the anterior chamber of the proventriculus (stomach) was removed for analysis. Prior to investigation of the stomach content, a subjective estimate of stomach fullness was made according to the methods described by Hynes (1950) and Hyslop (1980). Accordingly, stomachs were categorised as being empty (0%), partially full (25%), half full (50%), full (75%) or very full (100%).

The content of each stomach was emptied and suspended in dilute alcohol (Williams, 1981) and placed on a microscope slide. Contents were identified to the lowest taxonomic level practicable using standard keys. Stomach contents were rarely identifiable to species level and thus the data were grouped to higher taxonomic levels to facilitate comparison with other studies (Sitts & Knight, 1979; Siegfried, 1982; González-Ortegón et al., 2010). Contents were counted and the points scoring method pioneered by Swynnerton and Worthington (1940) and Frost (1943) was used to estimate the proportion of a prey item in the stomach.

In order to obtain a quantitative assessment of the importance of various food items frequency of occurrence and percentage of occurrence indices were calculated as follows:

$$\text{Frequency of occurrence (F):} \quad F = (n \times 100)/N_s$$

$$\text{Percentage of occurrence (P):} \quad P = (n' \times 100)/N_p$$

Where:  $n$  = total number of stomachs containing prey item  $x$ ;  $N_s$  = total number of stomachs examined;  $n'$  = total number of individuals of prey item  $x$ ;  $N_p$  = total number of prey items. These indices have been extensively employed in other studies of diet content in shrimp (Sitts & Knight, 1979; Siegfried, 1982; Karani et al., 2005; Kitsos et al., 2008) as well as other decapod crustaceans (Williams, 1981).

Vacuity coefficients (Fanelli & Cartes, 2004; Karani et al., 2005) were calculated for each species/sex/season combination, in order to provide a comparison of stomach fullness, using the following metric:

$$\text{Vacuity Coefficient (V):} \quad V = (E_v \times 100)/N_s$$

Where:  $E_v$  = number of empty stomachs;  $N_s$  = number of stomachs examined.

Chi-squared ( $\chi^2$ ) calculations were conducted on the number of prey items observed in both summer and winter diets of both males and females of each species to investigate the null hypothesis that there is no association between the diets of *P. longirostris* and *P. macrodactylus*, i.e. their diets' are independent of one another. Chi-squared analysis was conducted using MINITAB®.

## Results

A total of 464 specimens from the summer period (91 ♂♂, 157 ♀♀ *P. longirostris*; 93 ♂♂, 122 ♀♀ *P. macrodactylus*) and 326 stomachs from the winter period (150 ♂♂, 176 ♀♀ *P. longirostris*; 132 ♂♂, 208 ♀♀ *P. macrodactylus*) were analysed for stomach content.

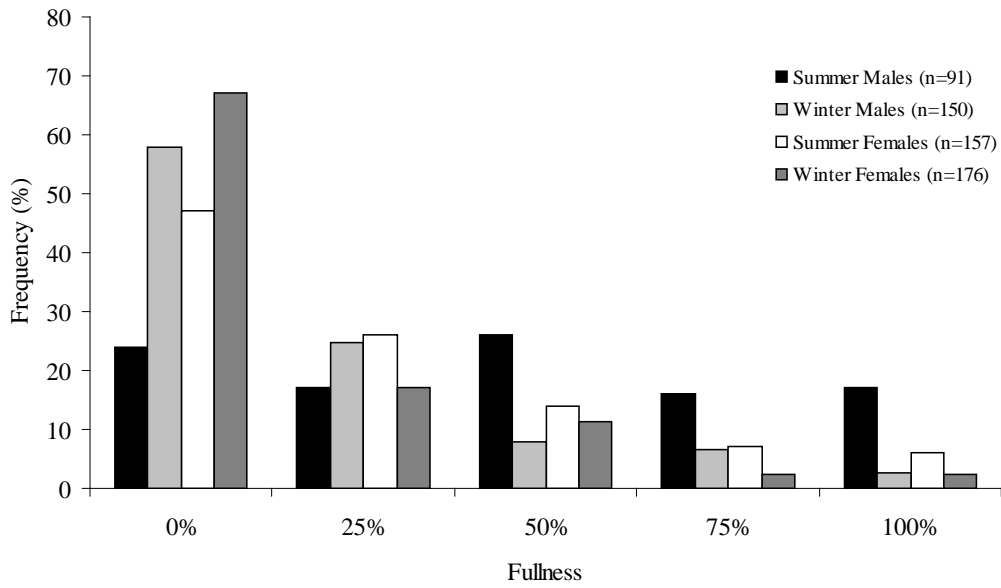
A total of 8113 identifiable prey items, assigned to 10 prey categories were retrieved from stomachs (Tables 4 and 7). All stomachs that contained prey also contained varying amounts of debris. The term debris is used here in keeping with Forster (1951a) in place of the more usual term detritus as it was not always possible to determine whether the material was organic or inorganic in origin. Amphipods and unidentified crustacean remains comprised the majority of the prey items encountered. Several prey items were identifiable to lower taxonomic levels, however in order to facilitate comparison with other studies and to other stomachs where specific identification was not possible they were combined under higher taxa. Those prey that were identifiable further included the amphipods *Apocorophium lacustre* (Vanhöffen, 1911), *Corophium volutator* (Pallas, 1766) and *Gammarus* spp., the mysid *Neomysis integer* (Leach, 1814) and the polychaete *Hediste diversicolor* (O.F. Müller, 1776).

Both species have a diverse diet consisting largely of crustaceans (Tables 4 and 7) but plant material and nereid polychaetes were also consumed by both species. Chironomid larvae and occasional fragments of sponges were present in stomachs during summer.

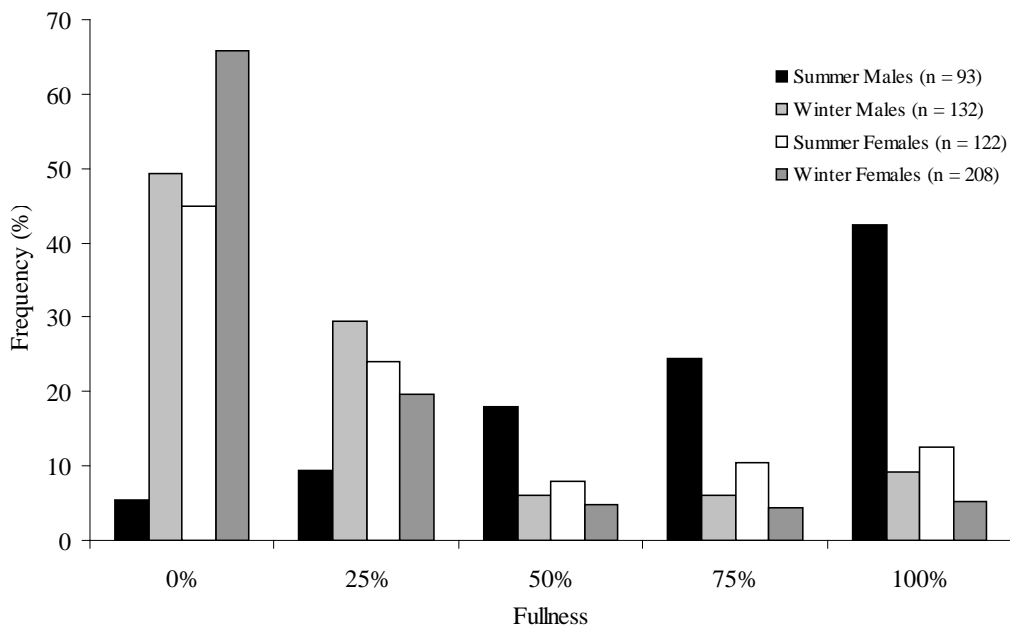
### *Stomach fullness and vacuity coefficients*

Both species examined here showed a greater frequency of full stomachs in summer than in winter (Figures 1 – 2) and males had a higher frequency of full stomachs than females (Figures 1 – 2) in both seasons.

Vacuity coefficients calculated for each species in each season are given in Table 1. Both species had higher vacuity coefficients in winter than in summer. Males of both species in summer had the lowest vacuity coefficients, whilst females in winter had the highest values of >65.



**Figure 1.** Stomach fullness of *Palaemon longirostris*.



**Figure 2.** Stomach fullness of *Palaemon macrodactylus*.

**Table 1.** Calculated vacuity coefficients for male and female *Palaemon longirostris* and *P. macrodactylus* in summer and winter.

		Total number of stomachs examined (N <sub>s</sub> )	Number of empty stomachs (E <sub>v</sub> )	Vacuity coefficient (V)
<i>Palaemon longirostris</i>				
summer	males	91	21	23.08
	females	157	73	46.50
winter	males	150	87	58.00
	females	176	118	67.05
<i>Palaemon macrodactylus</i>				
summer	males	93	5	5.38
	females	122	55	45.08
winter	males	132	65	49.24
	females	208	137	65.87

*Dietary analysis using the frequency of occurrence index*

Frequency of occurrence indices were calculated to investigate differences between males and females of each species in both summer and winter and also to investigate differences between *P. longirostris* and *P. macrodactylus* in both winter and summer.

Using this index, male *P. longirostris* consumed more mysids in both summer and winter, females consumed more decapods, barnacles, nereids and plant material (Table 2). Females consumed more amphipods in the summer than males but the situation was reversed in the winter. Unidentified crustacean remains accounted for more of the diet in males in the summer but females in the winter. More decapods were consumed in the summer and chironomid larvae, sponges and barnacles were only present in the summer diets.

**Table 2.** Diet composition of male and female *Palaemon longirostris* using the frequency of occurrence index.

<b>Summer</b>	Males			Females		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	23	71	32.39	16	81	19.75
Amphipoda	10	71	14.08	19	81	23.46
Decapoda	1	71	1.41	11	81	13.58
Nereididae	0	71	0.00	0	81	0.00
Chironomid larvae	7	71	9.86	8	81	9.88
Vascular plants and algae	1	71	1.41	5	81	6.17
Mysidae	7	71	9.86	5	81	6.17
Porifera	1	71	1.41	1	81	1.23
Cirripedia	0	71	0.00	2	81	2.47
Coleoptera	0	71	0.00	0	81	0.00
<b>Winter</b>	Males			Females		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	28	63	44.44	28	58	48.28
Amphipoda	21	63	33.33	17	58	29.31
Decapoda	0	63	0.00	2	58	3.45
Nereididae	2	63	3.17	6	58	10.34
Chironomid larvae	0	63	0.00	0	58	0.00
Vascular plants and algae	12	63	19.05	14	58	24.14
Mysidae	15	63	23.81	8	58	13.79
Porifera	0	63	0.00	0	58	0.00
Cirripedia	0	63	0.00	0	58	0.00
Coleoptera	0	63	0.00	0	58	0.00

In *Palaemon macrodactylus* (Table 3), males consumed more amphipods, decapods and nereids in both seasons. More plants and mysids were consumed by females. Plants and mysids became a more important food item for both sexes in the winter as did amphipods in the diet of males and unidentified crustacean remains in



the diet of females. Other prey were more frequent in the diet of summer shrimps than winter shrimps. As with *P. longirostris*, chironomid larvae, sponges and barnacles were only present in summer diets.

**Table 3.** Diet composition of male and female *Palaemon macrodactylus* using the frequency of occurrence index.

<b>Summer</b>	Males			Females		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	41	87	47.13	21	67	31.34
Amphipoda	35	87	40.23	21	67	31.34
Decapoda	23	87	26.44	15	67	22.39
Nereididae	10	87	11.49	7	67	10.45
Chironomid larvae	2	87	2.30	1	67	1.49
Vascular plants and algae	4	87	4.60	10	67	14.93
Mysidae	6	87	6.90	7	67	10.45
Porifera	1	87	1.15	1	67	1.49
Cirripedia	3	87	3.45	2	67	2.99
Coleoptera	0	87	0.00	0	67	0.00
<b>Winter</b>	Males			Females		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	24	67	35.82	31	71	43.66
Amphipoda	36	67	53.73	21	71	29.58
Decapoda	1	67	1.49	0	71	0.00
Nereididae	3	67	4.48	2	71	2.82
Chironomid larvae	0	67	0.00	0	71	0.00
Vascular plants and algae	17	67	25.37	28	71	39.44
Mysidae	9	67	13.43	17	71	23.94
Porifera	0	67	0.00	0	71	0.00
Cirripedia	0	67	0.00	0	71	0.00
Coleoptera	1	67	1.49	2	71	2.82

**Table 4.** Diet composition of *Palaemon longirostris* and *P. macrodactylus* using the frequency of occurrence index.

<b>Summer</b>	<i>Palaemon longirostris</i>			<i>Palaemon macrodactylus</i>		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	39	152	25.66	62	154	40.26
Amphipoda	29	152	19.08	56	154	36.36
Decapoda	12	152	7.89	38	154	24.68
Nereididae	0	152	0.00	17	154	11.04
Chironomid larvae	15	152	9.87	3	154	1.95
Vascular plants and algae	6	152	3.95	14	154	9.09
Mysidae	12	152	7.89	13	154	8.44
Porifera	2	152	1.32	2	154	1.30
Cirripedia	2	152	1.32	5	154	3.25
Coleoptera	0	152	0.00	0	154	0.00
<b>Winter</b>	<i>Palaemon longirostris</i>			<i>Palaemon macrodactylus</i>		
	n	N <sub>s</sub>	F	n	N <sub>s</sub>	F
Crustacean remains	56	121	46.28	55	138	39.86
Amphipoda	38	121	31.40	57	138	41.30
Decapoda	2	121	1.65	1	138	0.72
Nereididae	8	121	6.61	5	138	3.62
Chironomid larvae	0	121	0.00	0	138	0.00
Vascular plants and algae	26	121	21.49	45	138	32.61
Mysidae	23	121	19.01	26	138	18.84
Porifera	0	121	0.00	0	138	0.00
Cirripedia	0	121	0.00	0	138	0.00
Coleoptera	0	121	0.00	3	138	2.17

*Palaemon macrodactylus* consumed more amphipods and plant material than did *P. longirostris* in both summer and winter (Table 4). In summer *P. macrodactylus* also consumed more unidentified crustacean remains, decapods, nereids, mysids and barnacles. *Palaemon longirostris* consumed more chironomid larvae and sponges in summer, and more unidentified crustacean remains, decapods and nereids in the

winter than did *P. macrodactylus* (Table 4). Only *P. macrodactylus* consumed Coleoptera.

*Dietary analysis using the percentage of occurrence index*

Dietary analysis was also conducted by calculating percentage of occurrence indices. As with the frequency of occurrence indices differences between both sexes in both seasons for both species were investigated as well as interspecific differences.

The results obtained for the percentage of prey index for *P. longirostris* (Table 5) largely mirrored those obtained via the frequency of occurrence index. Differences were found in the percentage of chironomid larvae which formed a higher percentage of the diet of males and sponges which constituted a higher percentage of female diets in the summer. Females had a higher percentage of amphipod prey but a lower percentage of unidentified crustaceans remains in the winter.

Male *Palaemon macrodactylus* had a higher percentage of amphipod prey in both summer and winter, where females consumed more plants and mysids in both seasons (Table 6). The winter diet for both sexes corresponded with the results obtained for the frequency of occurrence index but differences were found in the summer diet where females consumed a higher percentage of decapods, nereids and chironomid larvae than males and males consumed a high percentage of sponges than females. The converse situation was obtained through the frequency of occurrence index.

**Table 5.** Diet composition of male and female *Palaemon longirostris* using percentage of occurrence index.

<b>Summer</b>	Males			Females		
	n'	N <sub>p</sub>	P	n'	N <sub>p</sub>	P
Crustacean remains	274	990	27.68	170	1001	16.98
Amphipoda	250	990	25.25	342	1001	34.17
Decapoda	24	990	2.42	126	1001	12.59
Nereididae	0	990	0.00	0	1001	0.00
Chironomid larvae	256	990	25.86	192	1001	19.18
Vascular plants and algae	4	990	0.40	27	1001	2.70
Mysidae	174	990	17.58	82	1001	8.19
Porifera	8	990	0.81	12	1001	1.20
Cirripedia	0	990	0.00	50	1001	5.00
Coleoptera	0	990	0.00	0	1001	0.00
<b>Winter</b>	Males			Females		
	n'	N <sub>p</sub>	P	n'	N <sub>p</sub>	P
Crustacean remains	172	760	22.63	90	507	17.75
Amphipoda	410	760	53.95	306	507	60.36
Decapoda	0	760	0.00	2	507	0.39
Nereididae	8	760	1.05	36	507	7.10
Chironomid larvae	0	760	0.00	0	507	0.00
Vascular plants and algae	63	760	8.29	44	507	8.68
Mysidae	107	760	14.08	29	507	5.72
Porifera	0	760	0.00	0	507	0.00
Cirripedia	0	760	0.00	0	507	0.00
Coleoptera	0	760	0.00	0	507	0.00

**Table 6.** Diet composition of male and female *Palaemon macrodactylus* using percentage of occurrence index.

<b>Summer</b>	Males			Females		
	n'	N <sub>p</sub>	P	n'	N <sub>p</sub>	P
Crustacean remains	541	1971	27.45	252	1545	16.31
Amphipoda	731	1971	37.09	560	1545	36.25
Decapoda	354	1971	17.96	357	1545	23.11
Nereididae	165	1971	8.37	130	1545	8.41
Chironomid larvae	16	1971	0.81	32	1545	2.07
Vascular plants and algae	24	1971	1.22	116	1545	7.51
Mysidae	100	1971	5.07	82	1545	5.31
Porifera	8	1971	0.41	4	1545	0.26
Cirripedia	32	1971	1.62	12	1545	0.78
Coleoptera	0	1971	0.00	0	1545	0.00
<b>Winter</b>	Males			Females		
	n'	N <sub>p</sub>	F	n'	N <sub>p</sub>	F
Crustacean remains	109	713	15.29	97	626	15.50
Amphipoda	442	713	61.99	265	626	42.33
Decapoda	1	713	0.14	0	626	0.00
Nereididae	65	713	9.12	36	626	5.75
Chironomid larvae	0	713	0.00	0	626	0.00
Vascular plants and algae	42	713	5.89	86	626	13.74
Mysidae	53	713	7.43	139	626	22.20
Porifera	0	713	0.00	0	626	0.00
Cirripedia	0	713	0.00	0	626	0.00
Coleoptera	1	713	0.14	3	626	0.48

Using the percentage of occurrence index to compare the diet of *P. longirostris* with *P. macrodactylus* (Table 7), very similar results were obtained to the frequency of occurrence index. The main differences found were in the consumption of mysids, which were found in a higher percentage in the diet of *P. longirostris* in summer and higher percentage of *P. macrodactylus* in the winter. This is the reverse

of the situation found by using the frequency of occurrence index. Likewise, *P. longirostris* consumed a higher percentage of amphipods in winter than did *P. macrodactylus* and *P. macrodactylus* consumed a higher percentage of nereids than did *P. longirostris* in the winter. The reverse was demonstrated using the frequency of occurrence index.

**Table 7.** Diet composition of *Palaemon longirostris* and *P. macrodactylus* using percentage of occurrence index.

<b>Summer</b>	<i>Palaemon longirostris</i>			<i>Palaemon macrodactylus</i>		
	n'	N <sub>p</sub>	P	n'	N <sub>p</sub>	P
Crustacean remains	444	1991	22.30	793	3516	22.55
Amphipoda	592	1991	29.73	1291	3516	36.72
Decapoda	150	1991	7.53	711	3516	20.22
Nereididae	0	1991	0.00	295	3516	8.39
Chironomid larvae	448	1991	22.50	48	3516	1.37
Vascular plants and algae	31	1991	1.56	140	3516	3.98
Mysidae	256	1991	12.86	182	3516	5.18
Porifera	20	1991	1.00	12	3516	0.34
Cirripedia	50	1991	2.51	44	3516	1.25
Coleoptera	0	1991	0.00	0	3516	0.00
<b>Winter</b>	<i>Palaemon longirostris</i>			<i>Palaemon macrodactylus</i>		
	n'	N <sub>p</sub>	F	n'	N <sub>p</sub>	F
Crustacean remains	262	1267	20.68	206	1339	15.38
Amphipoda	716	1267	56.51	707	1339	52.80
Decapoda	2	1267	0.16	1	1339	0.07
Nereididae	44	1267	3.47	101	1339	7.54
Chironomid larvae	0	1267	0.00	0	1339	0.00
Vascular plants and algae	107	1267	8.45	128	1339	9.56
Mysidae	136	1267	10.73	192	1339	14.34
Porifera	0	1267	0.00	0	1339	0.00
Cirripedia	0	1267	0.00	0	1339	0.00
Coleoptera	0	1267	0.00	4	1339	0.30

*Chi-squared ( $\chi^2$ ) analyses*

Chi-squared ( $\chi^2$ ) analyses were conducted to test the null hypothesis that diets of *P. longirostris* and *P. macrodactylus* are not associated with one another. Analysis was conducted on both summer and winter diets of each species (Table 8) as well as between males and female diets in each season for each species (Tables 9 and 10).

**Table 8.** Chi-squared analysis of summer and winter diets of *Palaemon longirostris* and *P. macrodactylus*.

<b>Summer</b>	<i>Palaemon longirostris</i>	<i>Palaemon macrodactylus</i>
Crustacean remains	observed < expected	observed > expected
Amphipoda	observed < expected	observed > expected
Decapoda	observed < expected	observed > expected
Nereididae	observed < expected	observed > expected
Chironomid larvae	observed > expected	observed < expected
Vascular plants and algae	observed < expected	observed > expected
Mysidae	observed > expected	observed < expected
Porifera	observed > expected	observed < expected
Cirripedia	observed > expected	observed < expected
<b>Winter</b>	<i>Palaemon longirostris</i>	<i>Palaemon macrodactylus</i>
Crustacean remains & Decapoda	observed > expected	observed < expected
Amphipoda	observed > expected	observed < expected
Nereididae	observed < expected	observed > expected
Vascular plants, algae & Coleoptera	observed < expected	observed > expected
Mysidae	observed < expected	observed > expected

There was a significant association between prey items consumed and *Palaemon* species in both summer ( $\chi^2 = 1086.429$ ,  $df = 8$ , P-Value = 0.0001) and winter ( $\chi^2 = 39.579$ ,  $df = 4$ , P-Value = 0.0001). The Chi-squared analysis demonstrated a high degree of separation in the summer diets with *Palaemon longirostris* showing a strong association with chironomid larvae, whilst *P.*

*macrodactylus* shows a greater association with decapods and nereids. In the winter diets differences in observed and expected values were less pronounced indicating less separation in winter. In both seasons, significant differences were also observed in the consumption of mysids with *P. longirostris* consuming more mysids in the summer and *P. macrodactylus* consuming more in winter; again this difference was less pronounced in the winter.

**Table 9.** Chi-squared analysis of male and female diets of *Palaemon longirostris* in summer and winter.

<b>Summer</b>	Male	Female
Crustacean remains	observed > expected	observed < expected
Amphipoda	observed < expected	observed > expected
Decapoda	observed < expected	observed > expected
Chironomid arvae	observed > expected	observed < expected
Vascular plants and algae	observed < expected	observed > expected
Mysidae	observed > expected	observed < expected
Porifera	observed > expected	observed < expected
Cirripedia	observed < expected	observed > expected
<b>Winter</b>	Male	Female
Crustacean remains & Decapoda	observed < expected	observed > expected
Amphipoda	observed > expected	observed < expected
Decapoda	observed < expected	observed > expected
Nereididae	observed < expected	observed > expected
Vascular plants, algae & Coleoptera	observed < expected	observed > expected
Mysidae	observed > expected	observed < expected

There were also significant associations of specific prey items with a specific sex in both summer (*P. longirostris*:  $\chi^2 = 20.758$ ,  $df = 7$ , P-Value = 0.005; *P. macrodactylus*:  $\chi^2 = 21.544$ ,  $df = 9$ , P-Value = > 0.005) and winter (*P. longirostris*:  $\chi^2 = 7.764$ ,  $df = 4$ , P-Value = > 0.05; *P. macrodactylus*:  $\chi^2 = 14.119$ ,  $df = 4$ , P-Value = > 0.01) but this was not as pronounced as those witnessed with species. In summer, significant differences were observed between males and females of both species in



the consumption of unidentified crustacean remains. *Palaemon macrodactylus* females also showed a significantly stronger association with chironomid larvae than males in the summer but this was not reflected in *P. longirostris*. In the winter male *P. macrodactylus* were more strongly associated with amphipods than were females. *Palaemon longirostris* male and females differed in their consumption of mysids in the winter and unidentified crustacean remains in the summer.

The results of the Chi-squared analyses show that there are greater differences in diet between species than between sexes of the same species. The results also indicate that there is a greater degree of separation between the diets' of the two species in the summer than in the winter. This indicates that whilst the diets appear not to be independent of one another in the winter (i.e. they show a strong degree of overlap), they are more independent in the summer. We cannot therefore completely reject the null hypothesis.

**Table 10.** Chi-squared analysis of male and female diets of *Palaemon macrodactylus* in summer and winter.

<b>Summer</b>	Male	Female
Crustacean remains	observed > expected	observed < expected
Amphipoda	observed < expected	observed > expected
Decapoda	observed > expected	observed < expected
Nereididae	observed > expected	observed < expected
Chironomid larvae	observed < expected	observed > expected
Vascular plants and algae	observed < expected	observed > expected
Mysidae	observed < expected	observed > expected
Porifera	observed < expected	observed > expected
Cirripedia	observed < expected	observed > expected
<b>Winter</b>	Male	Female
Crustacean remains & Decapoda	observed < expected	observed > expected
Amphipoda	observed > expected	observed < expected
Nereididae	observed > expected	observed < expected
Vascular plants, algae & Coleoptera	observed < expected	observed > expected
Mysidae	observed < expected	observed > expected

### Discussion

Stomach content analysis performed here on *Palaemon longirostris* and *P. macrodactylus* demonstrates that both species are largely carnivorous with amphipods, mysids and chironomid larvae forming a large proportion of the diet, the latter being restricted to summer diets. Plant and algal material were encountered only in a small number of stomachs concurring with the findings of several previous studies on *Palaemon* (Forster, 1951 a, b; Sitts & Knight, 1979; Berglund, 1980; Siegfried, 1982; Guerao, 1995; Guerao & Ribera, 1996). It is likely that plants and algae were ingested incidentally during predation (Guerao, 1995; Guerao & Ribera, 1996), or could have originated in the foreguts of consumed prey (Sitts & Knight, 1979), further evidenced by the fact that most stomachs that contained plant/algal material also contained other identifiable prey items.

The high proportion of crustacean remains in the stomachs may be partly attributable to their comparative resistance to digestion compared to more soft bodied animals (Siegfried, 1982). Likewise, nereid polychaetes, the only soft-bodied animals found in the stomachs, were mostly recorded through the presence of their chitinous jaws, paragnaths and chaetae, with traces of the softer portions found only in a few stomachs. However, some of the stomach content had evidently been recently ingested and included some soft body parts of nereids and crustaceans but no trace of other soft-bodied organisms was witnessed, so it would appear that this represents a genuine preference and that this study has provided an accurate representation of the diet of these two species in the River Thames.

As in other *Palaemon* species (e.g. Forster, 1951a; Janas & Barańska, 2008), small, regional differences reflecting localised differences in prey availability are observed between the present study and previous studies on the diet of these species. Previous studies on the diet of *P. macrodactylus* (Sitts & Knight, 1979; Siegfried, 1982; González-Ortegón et al., 2010) and *P. longirostris* (González-Ortegón et al., 2010) indicate that mysids form a large proportion of the diet of these species. In the present study, mysids were found to be an important prey item but not as dominant as reported in the earlier studies. This may simply be due to the fact that mysids are not abundant enough in this stretch of the Thames to form a major component of the diet. Little published data exists on the population dynamics of Mysidacea in the Thames

and, although they have been noted in other studies (e.g. Attrill & Thomas, 1996; Thomson Unicomarine unpublished data) they are not reported in high abundance which in turn determines their abundance in the diet of *Palaemon*. In contrast, amphipods are highly abundant throughout the Thames and were the dominant prey in the diet of both species investigated here. The dominant amphipods recorded were *Corophium volutator* and *Apocorophium lacustre*, both of which are highly abundant in the Thames, but in many cases these were not identifiable beyond family level. *Corophium volutator* is most abundant in muddy habitats (Meadows, 1964) whereas *A. lacustre*, whilst considered nationally scarce in the UK (Bratton, 1991), is locally abundant in the Thames particularly in the fouling community of submerged structures (CA pers. obs; Thomson Unicomarine unpubl. data). Corophiids were also considered an important part of the diet of *P. macrodactylus* in San Francisco Bay (Siegfried, 1982). Remains of gammarid amphipods were also recorded from the stomach analysis but in low numbers. Their comparative scarcity in the diet may in part be due to their more active lifestyles making them difficult to catch.

Newman reported evidence of cannibalism in *P. macrodactylus* when kept in crowded laboratory conditions (Newman, 1963). Whilst both species reported on here contained remains of unidentifiable decapods (most likely juvenile brachyurans) in their diet, compelling evidence for cannibalism, or even feeding on other carideans was lacking.

Chironomid larvae are a seasonally abundant prey item being found in high abundance during the summer. Chironomid larvae in temperate regions undergo strong seasonal variations with abundances being lowest during winter (Armitage et al., 1995) and therefore the absence in the diet of *Palaemon* during the winter was expected a priori. This may also account for some of the empty stomachs observed in winter samples as many stomachs examined from the summer samples contained only chironomid larvae and no other prey. Pérez-Bote (2006) also reported chironomid larvae as an important dietary element in shrimp and argued that they are preferentially selected due to their size and relative mobility. It should be noted that, whilst the study of Pérez-Bote (2006) was reported to be based on *Palaemonetes zariquieyi* Sollaud, 1939, a species of great relevance to the present study, Pérez-Bote (2008) later corrected the identification of the species concerned to *Atyaephyra desmaresti* (Millet, 1831).

Several other potential prey species that are highly abundant in the immediate vicinity of Tilbury Power Station were not recorded in the diet of either species investigated here. Oligochaetes are highly abundant throughout the Thames, with different species occurring in different sediments and salinity regimes, but were not encountered in the stomach content analysis. Their soft bodies may be more easily digested than those of crustaceans but if they were consumed then it seems likely that some evidence would have been found, especially given that some soft parts of other animals were found. More rigid-bodied animals that were also absent but would seem suitable prey include sphaeromatid isopods (*Lekanephaera* spp.) and gastropod molluscs (particularly *Potamopyrgus antipodarum*). *Potamopyrgus antipodarum* would provide an abundant and relatively slow moving food source on which to prey and molluscs have been recorded as prey in other diet studies of *Palaemon*. Siegfried (1982) reports occasional bivalves being present in the diet of *P. macrodactylus* and Forster (1951a) reports gastropods being common in the diet of *P. serratus*.

Sand was found to be present in many of the stomachs analysed. Although sand grains may have a bacterial film coating, this would provide only limited nutrition (Siegfried, 1982) and it is unlikely that it is intentionally selected as a food source. A more plausible explanation is that it is accidentally ingested with the desired prey or intentionally ingested to aid trituration. Likewise, although debris was present in many of the stomachs examined in this study, detritivory does not appear to be a major feeding strategy of *Palaemon* in the Thames, and much of the debris likely results from the breaking down of prey items (Forster, 1951a). In contrast, Janas and Barańska (2004) report detritus as the dominant component of the diet of *P. elegans* in the Baltic Sea.

Vacuity coefficients were high in both sexes of both species in winter samples and in females of both species in the summer. Overall they were higher in the winter samples suggesting that feeding slows in the winter. Possible causes of this are reduced activity and reproductive rates, and therefore decreased energy requirement, in the winter as well as probable reduction in prey availability in winter. Many of the specimens with empty stomachs in the summer samples were ovigerous supporting the contention that females do not feed whilst carrying eggs. Additionally, many of those with empty stomachs in late winter (February) samples had well developed gonads in agreement with Fanelli and Cartes (2004). However, contrasting with this, Kitsos et al. (2008) and Cartes and Sardá (1989) suggest that feeding is more intense

in females during winter as they gather resources necessary for reproduction. Forster (1951a) noted that stomach content was frequently lost if the specimens were placed into preservative whilst still alive and it is possible that this may account for some of the empty stomachs found during this study. Clearance rates are not available for *Palaemon* but Wilcox and Jefferies (1974) found that the stomach of *Crangon septemspinosa* was emptied within 6-12 hours of feeding. On the assumption of a similar clearance rate in *Palaemon* we may assume that specimens with content in their stomach had fed in the previous 12 hours.

An important aspect of the present study is the information it provides on the potential effects on native biota of the introduction of *P. macrodactylus*. *Palaemon macrodactylus* is a relatively recent arrival in the Thames (Ashelby et al., 2013) and its' occurrence with *P. longirostris* is still a new phenomenon, thus their interactions are not yet understood. Additionally, the extra pressure exerted by this species on trophic resources has not been investigated. Previous studies (Sitts & Knight, 1979; Siegfried, 1982; González-Ortegón et al., 2010) had suggested that we may find the greatest predation pressure on mysids, however, amphipods were found to be a more important food resource in the Thames.

One of the key findings of the present study is the indication of strong dietary overlap in the winter diet of *Palaemon macrodactylus* and *P. longirostris* suggesting that they are competing for food resources in the River Thames on a seasonal basis. This seasonal difference in dietary overlap may partly result from lower prey availability in the winter and the complete elimination of chironomid larvae from the diet in winter, which are one of the main prey items contributing to dietary separation in the summer diet. It is also possible that, if the original introduction of *P. macrodactylus* occurred in the summer when the two diets show less overlap, this may have provided the species with an advantage in establishing as there would have been less competition for food than in winter.

Whilst dietary overlap has already been demonstrated between the two species in the Guadalquivir Estuary, Spain by González-Ortegón et al. (2010), Béguer et al. (2011) indicated that *P. macrodactylus* exploits niches in the Gironde Estuary, France that are currently under-used by *Palaemon longirostris* thus reducing competition. However, the results of the present study suggest that they occupy overlapping niches, at least on a seasonal basis. Colwell and Futuyma (1971) define an overlapping niche as the shared use of resources by two or more species. However, occupying the same

niche does not in itself indicate competition is occurring, if abundant enough food is present. Competition will only occur if the food resource becomes limiting (Steinwascher, 1981). Attrill et al. (1999) demonstrated long term decrease in the abundance of *Gammarus* spp. in the Thames Estuary, suggesting that the bulk of the population may have migrated upstream. However, other possibilities include pollution, drought or climate change related changes in abundance. Such changes in abundance of potential prey items, particularly those showing the greatest influence in the summer (decapods, nereids and chironomid larvae) may increase the potential for significant levels of competition between *P. macrodactylus* and *P. longirostris*.

The data presented here indicate a diverse diet of both *Palaemon longirostris* and *P. macrodactylus* in the River Thames. Both species are predominately carnivorous with amphipods forming a large proportion of the diet. The high degree of trophic overlap demonstrated in winter samples in this study indicates that the two species compete for food resources in the River Thames in the winter but less so in the summer. If food resources become limited, particularly in the summer, then *P. macrodactylus* may have a damaging effect on *P. longirostris*.

### Acknowledgements

R. Kowalik of the Zoological Society of London and her colleagues are thanked for establishing the monitoring program at Tilbury Power Station and having the forethought to provide decapod specimens for further analysis to supplement their original study. Thomson Unicomarine partially supported the work of the first author.

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## General Discussion



## General Discussion

The caridean shrimp genus *Palaemon* is widely reported in the scientific literature and is familiar to many scientists and amateur naturalists, however several aspects of this genus remain poorly known. The studies presented here have concentrated on a number of different aspects of the biology, morphology, taxonomy and systematics of *Palaemon*. The genus has shown itself to be morphologically conservative, highly adaptable and to show a high degree of intrageneric overlap in range, diet and life history traits (e.g. Holthuis, 1950; Forster, 1951a, 1951b; Pereira, 1997; González-Ortegón et al., 2010; Vázquez et al., 2012 and references therein).

The taxonomy of the genus, and indeed the subfamily Palaemoninae, is far from settled. The taxonomy of *Palaemon* presents an enigma, with species being paradoxically morphologically conservative in many characters found to be of value in other caridean families and highly variable in other characters. Many of the characters historically regarded as being species specific characters of *Palaemon* show a high degree of variation within single species, one of the most obvious being variation in the dentition of the rostrum (e.g. Yaldwyn, 1957; De Grave, 1999). Here, a number of characters, such as the presence or absence of a pre-anal spine or the shape of the 5<sup>th</sup> and 6<sup>th</sup> pleurae, that have either not been previously used or have not been attributed significance in the taxonomy of *Palaemon* have been shown to be of value in diagnosing species. Two new species described as part of this study were partially defined using a combination of these characters and it is recommended that subsequent descriptions or redescriptions of *Palaemon* species include these characters in addition to those more traditionally used.

Likewise, some of the characters currently defining palaemonine genera have also been demonstrated to be of little taxonomic significance through the molecular study undertaken here. This is in agreement with previous molecular (Murphy & Austin, 2005; Wowor et al., 2009) and morphological (Pereira, 1997) studies on the subfamily and with the hypothesis that *Palaemon* as presently defined is a paraphyletic genus. This paraphyly is caused by the inclusion of the genera *Palaemonetes*, *Exopalaemon* and *Coutierella* and the exclusion of *P. pandaliformis*, *P. gracilis* and *P. concinnus*. The study recovered strong support for geographic relationships but little evidence to support generic relations. A later study by Cuesta et al. (2012) also recovered geographic clades but included fewer taxa. Their

statement that *Palaemon* and *Palaemonetes* recover as monophyletic within Europe seems to merely reflect the recovery of a European clade, as found in this study.

Both the morphological taxonomic work and the molecular work indicate that a reappraisal of both specific and generic level characters is required. So what is to become of the future taxonomy and systematics of the genus? Perhaps the most satisfactory answer is to follow up the molecular work with a full cladistic analysis based on morphological characters. The only morphological phylogeny for the subfamily produced to date is that of Pereira (1997). Whilst Pereira (1997) also demonstrated the paraphyly of *Palaemon*, this study differed in several respects from the molecular analysis presented here which is possibly attributable to the characters chosen or to taxon sampling. Several of Pereira's (1997) characters have subsequently proved variable or have overlapping conditions making polarisation of the characters difficult. More recent phylogenetic software packages (e.g. TNT – Goloboff et al., 2008) have been developed with the potential for using continuous characters in mind and may therefore be more appropriate for an analysis of *Palaemon*. Should the results of such an analysis confirm the clades recovered in the molecular work then it would enable the morphological basis for these clades to be elucidated, enabling greater emphasis on these characters in subsequent taxonomic descriptions. Additionally, species that were not included in the molecular study either due a lack of material or the fact that the available material was not suitable for molecular analysis could be included in a morphological study based on literature accounts. Further molecular work using a larger suit of genes (Page et al., 2008) may also be considered to further confirm or refute these relationships. Such an integrative multi-disciplinary approach has been suggested to resolve systematic relationships elsewhere in the Caridea (Li et al., 2011).

Another approach for investigating species level differences would be to apply geometric morphometric analyses, as applied in this study to investigate two reported forms of *Palaemon longirostris*. Several aspects of this sort of analysis may provide advantages in the study of *Palaemon*. Firstly, it can quantify shape related differences which may be of importance in the absence of definitive or non-overlapping characters. Secondly, it would enable an image bank to be created (Riedlecker et al., 2009) with which any suspected new species could be compared. Average shape, composite images can be produced or alternatively extremes of form can be easily displayed (Riedlecker et al., 2009) which may not be reflected by line drawings



created from a single specimens. Line drawings would still be required to provide more detail to features which may be lost in the average shape configurations produced by most current geometric morphometric software. A disadvantage of using geometric morphometrics in the description of new species is that it can require large sample sizes. Saila & Martin (1987) suggest that the number of specimens included should be at least three times the number of landmarks. Many species are described from unique or small numbers of specimens especially where the species concerned live in cryptic habitats or may be considered to be vulnerable. Despite the fact that geometric morphometric methods do not require sacrificing the specimens such species may be unsuitable for this analysis.

One question of prime importance to biologists is how the features and characters described by taxonomists relate to their function. Here the function of the mandible across a range of palaemonoid shrimps was inferred from analysis of their structure using a scanning electron microscope. The results were consistent with the hypothesis that the form of the mandible is influenced largely by diet and conveys only limited phylogenetic information. Species with specialised diets have correspondingly specialised mouthparts. Further, the mouthparts are not independent of one another but rather work in concert during feeding. The function of each particular mouthpart may not unique to that mouthpart and the same function may be conducted by different mouthparts in different species (Borradaile, 1917). One unexpected outcome of this study was the diversity in form, structure and arrangement of cuticular structures. Whether these also convey generic level phylogenetic information may be answered through the examination of additional species within each of the genera analysed. However, many of the species in the genera investigated have similar diets and teasing apart differences caused by diet from phylogenetic influence may be difficult. Previous evidence suggests that the arrangement of cuticular structures in *Palaemon* is species specific (Fujino & Miyake, 1968).

The regional study of the non-*Macrobrachium* Palaemoninae fauna of Taiwan recorded 13 species belonging to seven genera. This compares favourably with other Asian regional studies (with *Macrobrachium* spp. excluded) for example 10 species from five genera for Vietnam (Nguyễn, 1992, 1997, 2000), 15 species from six genera from the Philippine-Indonesian region (Chace & Bruce, 1993) and 26 species from eight genera from mainland China (Li et al., 2007), with high levels of species overlap occurring between these studies. The comparatively high number of species in the

latter study is largely a function of larger area covered by that synopsis and the diversity of habitats that provides.

Two distinct morphotypes of *Palaemon serrifer* were found to occur in Taiwan. Subsequently, one of the forms of *P. serrifer* that occurs in aquaculture ponds in Donggang was included in the molecular phylogenetic analysis. This latter study demonstrated significant differences in both the 16SrRNA and H3 sequences from this population to those of a specimen from Korea and in the 16SrRNA sequence from a specimen from Singapore. This strongly suggests that *P. serrifer* as presently defined represents a species complex and that the specimens from Taiwan represent an undescribed species. The specimens from Taiwan differ largely in the form of their rostrum but do fall within the range of variation for *P. serrifer* reported in the literature (Kubo, 1942; Holthuis, 1950; Nguyễn, 1992). Elucidating the specific level differences of this form requires further work and, as discussed above, a combined approach of traditional taxonomic techniques, genetic evidence and a geometric morphometric analysis would perhaps be the best method of determining the identity of this species.

Several anthropogenic factors may complicate future investigations into the taxonomy of *Palaemon*. Recently morphological abnormalities have been reported in specimens of *P. longirostris* and *P. macrodactylus* from the Gironde Estuary, France Béguer et al. (2008, 2010). These abnormalities were also noted in specimens from other European estuaries but at a lower incidence of occurrence. Occasional, natural malformations are reported in the literature (e.g. Fauvel, 1900; Aguirre & Hendrickx, 2005; De Grave & Mentlak, 2008; Ashelby & Lavesque, 2011) and are regarded as a scientific curiosity. However, the high rate and nature of the deformities reported by Béguer et al. (2008, 2010) suggested a more serious underlying cause. Béguer et al. (2008, 2010) speculate that the most likely cause of the deformities is toxic metal pollution. The specimens from the Gironde are sometimes so mutated that species identification is almost impossible (pers. obs.) which could further complicate ecological, population or environmental assessment studies.

A further anthropogenic factor that may cause confusion in the identification of *Palaemon* is the human mediated introduction of animals. Animals introduced outside of their native range may not always be recognised in their new environments as different from their congeners. This has certainly been the case with *Palaemon macrodactylus* which has been introduced to six different regions globally outside of

its native range but in nearly every case has been overlooked for several years before being recognised. Analysis of archived material has invariably antedated the first noted occurrences in a region. For example, in Europe the species was present for over a decade before being recognised and formally reported (Worsfold & Ashelby, 2008). Whilst other species of Caridea have also been introduced outside of their native range (e.g. Emmet et al., 2002; De Grave & Ghane, 2006; Salman et al., 2006; Zare et al., 2010; Pachellet et al., 2011; Silva-Oliveira et al., 2011; Taylor & Komai, 2011; De Grave & Mann, 2012; Almeida et al., 2012), *P. macrodactylus* has been the most widely reported. The potential effects of the introduction of *P. macrodactylus* are still poorly understood but very few introductions are truly benign. Under current conditions its effect on native communities appears limited but introduced species may act as ticking time bombs waiting until a change in conditions gives them a competitive edge (Simberloff, 2010). In this study, a seasonal dietary overlap was demonstrated between *P. macrodactylus* and the native *P. longirostris* in the River Thames. Overlapped in winter, when food resources are more limited, but showed a greater degree of separation in the summer. Whilst food sources are abundant this overlap may not have any deleterious effect on the native species, however if there was a decline in food resources, perhaps in combination with other factors that put additional stress on the animals, then *P. macrodactylus* may gain an advantage and out-compete *P. longirostris* for food. It is also suggested here that an introduction event of *P. macrodactylus* to the Thames in the summer, when diets show a greater degree of separation, may be more likely to result in a successful colonisation due to the reduced competition for food. Another species of *Palaemon* that has begun a global invasion is *P. elegans* that has previously been introduced into the Caspian Sea (Zenkevich, 1963; Grigorovich et al., 2002), Iraq (Holthuis & Hassan, 1975) and most recently into north-western Atlantic waters (J. Carlton, pers. comm.). This mirrors the pattern set by other invasive decapod genera such as *Hemigrapsus* (reviewed by Bockerhoff & McLay, 2011) and *Eriocheir* (Jensen & Armstrong, 2004; Bentley, 2011; Naser et al., 2012) where first one species begins invading, followed by further species. This pattern suggests that, rather than individual species being prone to invading it is actually the genus that possesses the biological traits necessary for successful invasion. Given this, we can only speculate on which *Palaemon* species may be introduced next and to which region.

Climate change is also having a huge effect on natural biological communities (Laubier, 2001). Not only is this allowing range extensions to occur and for populations of warmer water animals to move north- or southwards (depending on the hemisphere) but it also increases the chances of invasion by introduced species as already stressed communities may be less able to resist an invader (Occhipinti-Ambrogi, 2007).

One advantage that *Palaemon* may have over other shrimp genera to take advantage of climate change and human activities is their broad environmental tolerance to changes in salinity, temperature and hypoxia (e.g. Born, 1968; Campbell & Jones, 1989; González-Ortegón, 2006) which would enable them to adapt, or at least tolerate changes in environmental conditions. This broad tolerance and physiological plasticity has also been expressed in the evolutionary history of the group with repeated invasions of freshwater as demonstrated by the molecular phylogeny conducted herein.

This study has demonstrated that *Palaemon* are paradoxically morphologically conservative and highly variable within a species. They are taxonomically and systematically confused and the suggestion is made that future taxonomic works take into account new techniques or other lines of evidence. *Palaemon* have also demonstrated themselves to be adept at invading both in evolutionary terms with multiple habitat transitions to freshwater as well as in contemporary terms in association with human activities. These invasions probably reflect the animals high degree of environmental tolerance and physiological plasticity.

This research should not be seen as an end-point itself, rather it is hoped that it will stimulate further investigations and be a solid foundation for future studies.

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