

Preliminary study of the preungual process in the Paguroidea, with emphasis on the Paguridae (Crustacea: Decapoda: Anomura)

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Abstract

The fourth pereopods in the Paguroidea are considerably reduced in size, with propodi and dactyls uniquely modified for use inside a variety of shelters. In many Paguridae and some Diogenidae, the dactyl is provided with an intriguing structure known as the preungual process, located at the base of the corneous claw. This structure was discovered in 1969 in species of *Solenopagurus* de Saint Laurent and *Catapagurus* A. Milne-Edwards by French carcinologist M. de Saint Laurent, who hypothesized that it had a sensory function. Since then, a similar although not necessarily homologous process has been found in species of 22 (or 29%) of the 76 genera in the Paguridae, and 3 (or 15%) of the 20 genera in the Diogenidae. The microstructure of the preungual process is described in detail for the first time in nine species of Paguridae, based on preliminary SEM and light microscopy observations. In these species, the process is variable in size and shape depending on the species, and can consist of a naked conical protuberance or a tube-like structure with simple or complex seta-like filaments in various degrees of density. The ontogenetic origin and phylogenetic significance of the process as well as any habitat or other environmental factors that may influence its development, remain to be investigated.

Key words: preungual process, Paguroidea, *Phimochirus*, *Catapagurus*, *Enallopagurus*, *Icelopagurus*, *Lophopagurus*.

Introduction

Numerous sensory structures have been documented in decapod crustaceans, although most frequently studies have focused on lobsters (Astacidea), and the true crabs (Brachyura) (*e.g.*, Ache, 1982; Bush and Laverack, 1982; Atema and Voigt, 1995; Lavalli and Spanier, 2007). In hermit crabs (Paguroidea sensu McLaughlin *et al.*, 2007), many studies have documented sensory structures found on the eyes, antennae and antennules (*e.g.*, Jackson, 1913; Makarov, 1938, 1962; Ghirardella *et al.*, 1968; Ghirardella *et al.*, 1973; Snow, 1973, 1974), whereas in few studies have the presence of similar structures on other appendages or external parts of the body been investigated. Field (1974) studied the morphology of hair sensilla,

proprioceptors, and chordotonal organs, and the role these have in cheliped flexion behavior on the chelipeds of *Pagurus ochotensis*. McLaughlin and Brock (1974) found sensory-modified spines on the dorsal surfaces of the chelae and carpi of the chelipeds in the Hawaiian species *Nematopagurus spinulosensoris* McLaughlin and Brock, 1974. Subsequently McLaughlin and Lane (1975) described in detail the morphology of these unique spines, and hypothesized that these might be used to detect and repel predators. McLaughlin (1997) described somewhat similar structures on the spines of the chelae in *Pagurus capsularis* McLaughlin, 1997 and *P. pergranulatus* (Henderson, 1896), but the paucity of material available to her precluded a more detailed investigation. Mesce (1993) found four types of cuticular structures on the surface of

the minor chela of *P. hirsutiisculus* Dana, 1851, two of which (setal tufts, and corneous teeth on the cutting edge of the dactyl) functioned as mechanoreceptors and/or chemoreceptors during shell selection, whereas two other types (tubercles, and minute pits around setal tufts) had unclear functions.

The fourth pereopods in the Paguroidea are considerably reduced in size, with propodi and dactyls uniquely modified (Fig. 1). In most species, this pereopod is weakly semichelate, with the propodus provided with a rasp that varies in degree of development, and is made of one to numerous rows of corneous scales. The dactyl has a lateroventral row of corneous teeth, and terminates in a corneous claw. In some Paguridae and a few Diogenidae, the dactyl is also provided with an intriguing structure known as the preungual process, located at the base of the corneous claw. This structure was first documented by de Saint Laurent (1970) for species of *Solenopagurus* de Saint Laurent, 1968 and *Catapagurus* A. Milne-Edwards, 1880, and who named it “processus préunguéal”, hypothesizing that it had a sensory function. Since then, similar processes have been reported in species of 22 (or 29%) of the 76 genera in the Paguridae, and 3 (or 15%) of the 20 genera in the Diogenidae, although not always consistently present or absent in all representatives of each genus.

Despite the many reports of preungual processes in taxonomic works (*e.g.*, de Saint Laurent, 1970; McLaughlin, 1974, 1997, 2003; Lemaitre and McLaughlin, 2003; Asakura, 2004, Asakura and Kosuge, 2004), only brief descriptions of these processes have been included, and details of individual morphologies have not been documented. However, it is clear from these taxonomic works that while hermit crab preungual processes may be positionally homologous among taxa, they are not identical, nor are they always morphologically similar. For example, the diogenid preungual processes illustrated for two species of *Paguristes* Dana, 1851 by Komai (2001) are neither positionally nor morphologically similar to the structures illustrated by Asakura (2004) and Asakura and Kosuge (2004) for two *Pseudopaguristes* McLaughlin, 2002 species, and all differ substantially from pagurid preungual processes. Variability in this process among pagurids is manifest both morphologically and in intra-generic occurrence. In only a few populous genera such as *Catapagurus*, *Phimochirus* McLaughlin, 1981 and *Pylopagurus* A. Milne-Edwards and Bouvier, 1893, are all recognized species characterized by possession of preungual processes, and as yet no common denominator has been found to explain their occurrences.

Based on literature accounts, it is obvious that one description does not fit everything that

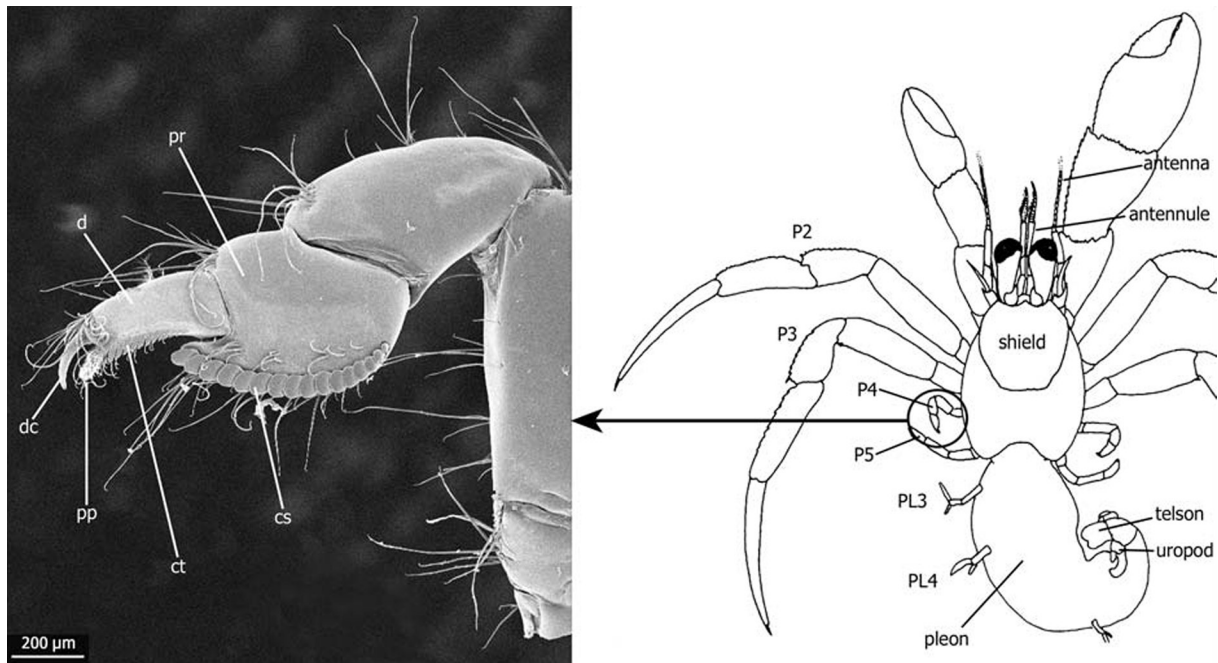


Figure 1. Diagrammatic Paguridae and micrograph of left fourth pereopod (lateral view) of *Phimochirus holthuisi* (Provenzano, 1961), showing location of preungual process and other parts of propodus and dactyl mentioned in text. Abbreviations: cs, corneous scales of propodal rasp; ct, corneous teeth; d, dactyl; dc, dactylar claw; P, pereopod; PL, pleopod; pp, preungual process; pr, propodus.

has been alluded to as a preungual process. This puzzling structure seems to occur in some genera as what appears to be a mere enlargement (often obscurely visible) of a corneous scale at the base of the dactylar claw, whereas in its well developed form in other genera it appears to be a complex sensory structure as suggested by its elaborate ornamentation (e.g., Fig. 2). For the purpose of this preliminary study, we have included several genera and species in which development of a preungual process has reached a sufficiently advanced level to permit recognition as a clearly distinct entity apart from the dactylar teeth or setae. Our emphasis in the present study has been on the examination of the preungual process in *Phimochirus holthuisi* (Provenzano, 1961) through SEM, and light mi-

croscopy, but two other species of *Phimochirus* and five species in five additional genera have been examined to lesser degrees and are included to illustrate the diversity already recognized in this structure.

Material and Methods

The preungual process in nine species of Paguridae was studied using SEM and/or light microscopy techniques. All specimens studied and figured in SEM micrographs were adults or sexually mature. No significant variations in morphology of the preungual process related to sex were detected. Specimens for this study

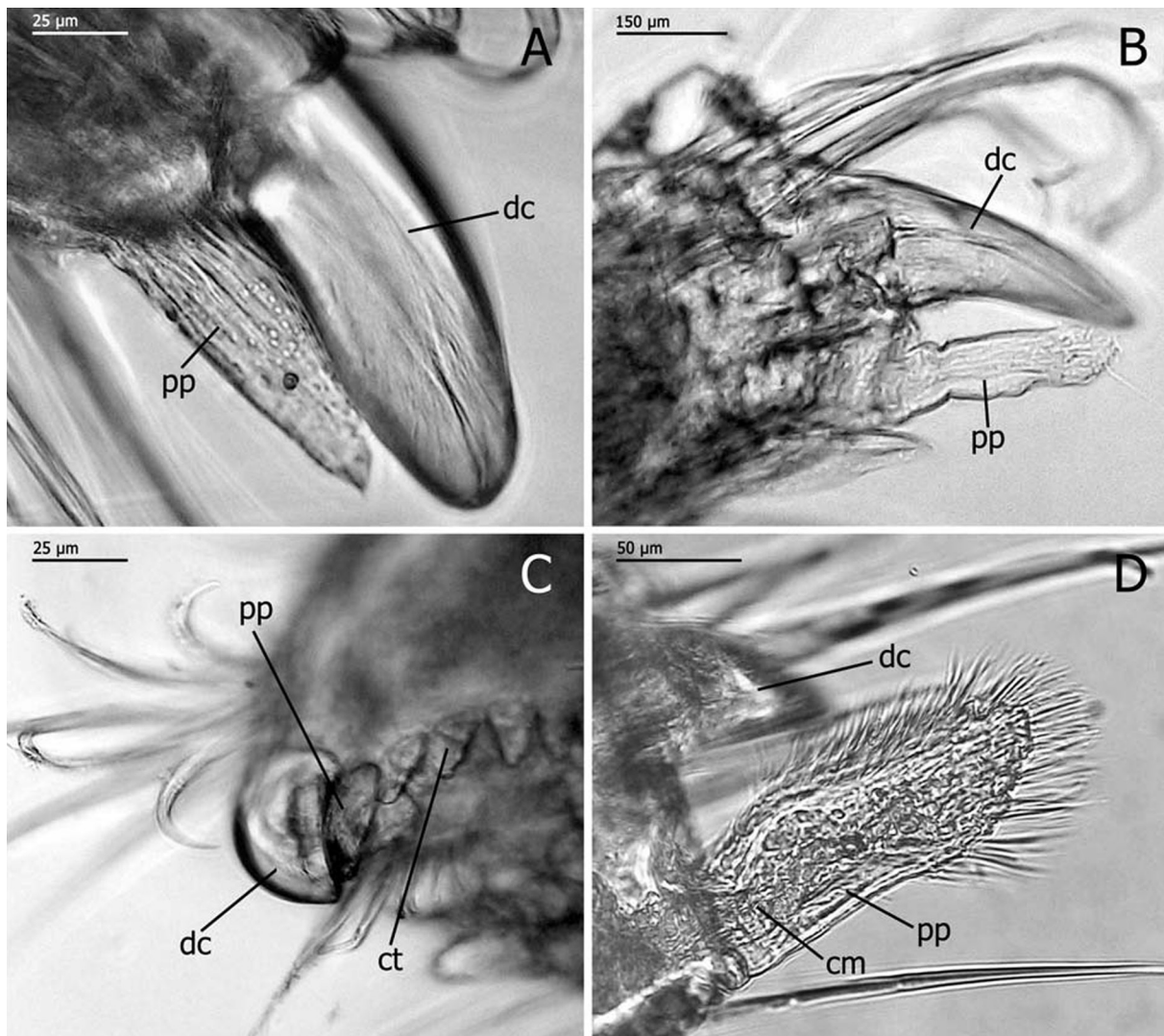


Figure 2. Light microscopy photographs of distal region of dactyl of left fourth pereopod (mesial view except for C, lateroventral view): A, *Enallopagurus spinicarpus* (Glassell, 1938) (USNM 285442); B, *Icelopagurus crosnieri* McLaughlin, 1997 (USNM 291238); C, *Manucomplanus spinulosus* (Holthuis, 1959) (USNM 275937); D, *Catapagurus sharreri* A. Milne-Edwards, 1880 (USNM). Abbreviations as in Fig. 1, except for cm, cellular material.

have come from the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Virginia Key, Florida (RSMAS). The SEM micrographs were taken by Kim Wilson at the facilities of Florida International University, Tamiami Campus, Florida (FIU) under the supervision of George Taylor, and by Sarah Trunnell at the USNM SEM Lab under the supervision of Scott Whittaker. The light microscopy photographs were obtained using a Sony Handycam HDR-HC3 Digital HC Video Camera Recorder attached to a Meiji Techno MX 5000 compound microscope.

Results

Light microscopy observations

Light microscopy observations were done in specimens of five species. While these observations show only limited details on the external and internal morphology of the preungual process, they do provide useful insight into the complexity of this process.

In *Enallopagurus spinicarpus* (Glassell, 1938), a species distributed in the eastern Pacific, from the west coast of Baja California, Mexico, and the Gulf of California, to Colombia, in depths ranging from 19 to 175 m (McLaughlin, 1982), the preungual process (Fig. 2A) is elongate and conical, and extends for about 0.9 the ventral length of the dactylar claw. The process terminates in a pointed tip, and does not appear to have any seta-like filaments. However, in at least another species of *Enallopagurus*, the process is more complex than in *E. spinicarpus* (see SEM observations under *Enallopagurus* sp.).

In *Icelopagurus crosnieri* McLaughlin, 1997, a species found in the tropical western Pacific, from the Tanimbar Islands, Indonesia, in depths ranging from 884 to 891 m (McLaughlin, 1997), the preungual process (Fig. 2B) consists of a slender, semi-transparent and flexible tubular projection that extends nearly to the tip of the dactylar claw. The process is rounded distally, and can be naked or have moderately dense and seta-like filaments distally, although these are not always clearly visible using light microscopy.

In *Manucomplanus spinulosus* (Holthuis, 1959), a rare species known so far only from the Straits of Florida, the southern Caribbean, and Suriname on northeastern South America, in depths of 24 to 108 m (Lemaitre and McLaughlin, 1996), the preungual process (Fig. 2C) is a short, stout conical projection extending for about half to three-fourths the ventral length of the dactylar claw, and terminates in a blunt tip. The process is located under the base of the dactylar claw, and close to the distal corneous tooth on the latero-ventral row of teeth of the dactyl. No seta-like filaments are apparent.

In *Catapagurus sharreri* A. Milne-Edwards, 1880, a species broadly distributed in the western Atlantic from off Massachusetts, USA, through Florida and Gulf of Mexico, to Brazil (Felder *et al.*, 2009), in depths of 80 to 694 m, the preungual process is well developed. The process (Fig. 2D) consists of a prominent, semi-transparent tubular and somewhat flexible projection that distinctly exceeds the dactylar claw. It is distally rounded, and densely covered distally with relatively long seta-like filaments. Internally, there appears to be a core of cellular material in the dactyl that is included in or discharged into the preungual process.

SEM observations

SEM techniques were used to make observations of the preungual process in specimens of five species. These provided much greater detail of the external morphology of this process than did light microscopy.

In *Phimochirus holthuisi* (Provenzano, 1961), a species broadly distributed in the tropical and subtropical regions of the western Atlantic from the eastern coast of the United States, the Gulf of Mexico, and Caribbean, to northern Brazil, in depths ranging from 1 to 291 m (McLaughlin, 1981), the preungual process (Figs. 1, 3) consists of an elongate, tubular projection extending to about three-fourths the length of the dactylar claw. The basal portion of the process is naked, whereas distally it is densely covered with flat, seta-like filaments, some of which are distally split into multiple tips. A few short, transverse or oblique rows of short, seta-like filaments are present on the median portion of the process.

In *Phimochirus operculatus* (Stimpson, 1859), a relatively rare species known so far from the

tropical western Atlantic, from South Florida and the southern Caribbean (Curaçao and Colombia), in depths ranging from the intertidal to 15 m (McLaughlin, 1981), the preungual process (Fig. 4) is a prominent, tubular projection extending to about three-fourths the length of the dactylar claw. The distal portion of the process consists of a dense brush of flat, seta-like filaments, and the remainder is naked.

In *Phimochirus randalli* (Provenzano, 1961), a species known from the tropical western Atlantic (Bahamas Islands, Straits of Florida, Gulf of Mexico, and Caribbean Sea), in depths ranging from 15 to 91 m (McLaughlin, 1981; Lemaitre and McLaughlin, 2003), the corneous claw of the dactyl is short and located on the dorsodistal margin of the dactyl. The preungual process is on the ventrodistal margin of the dactyl, and consists of a

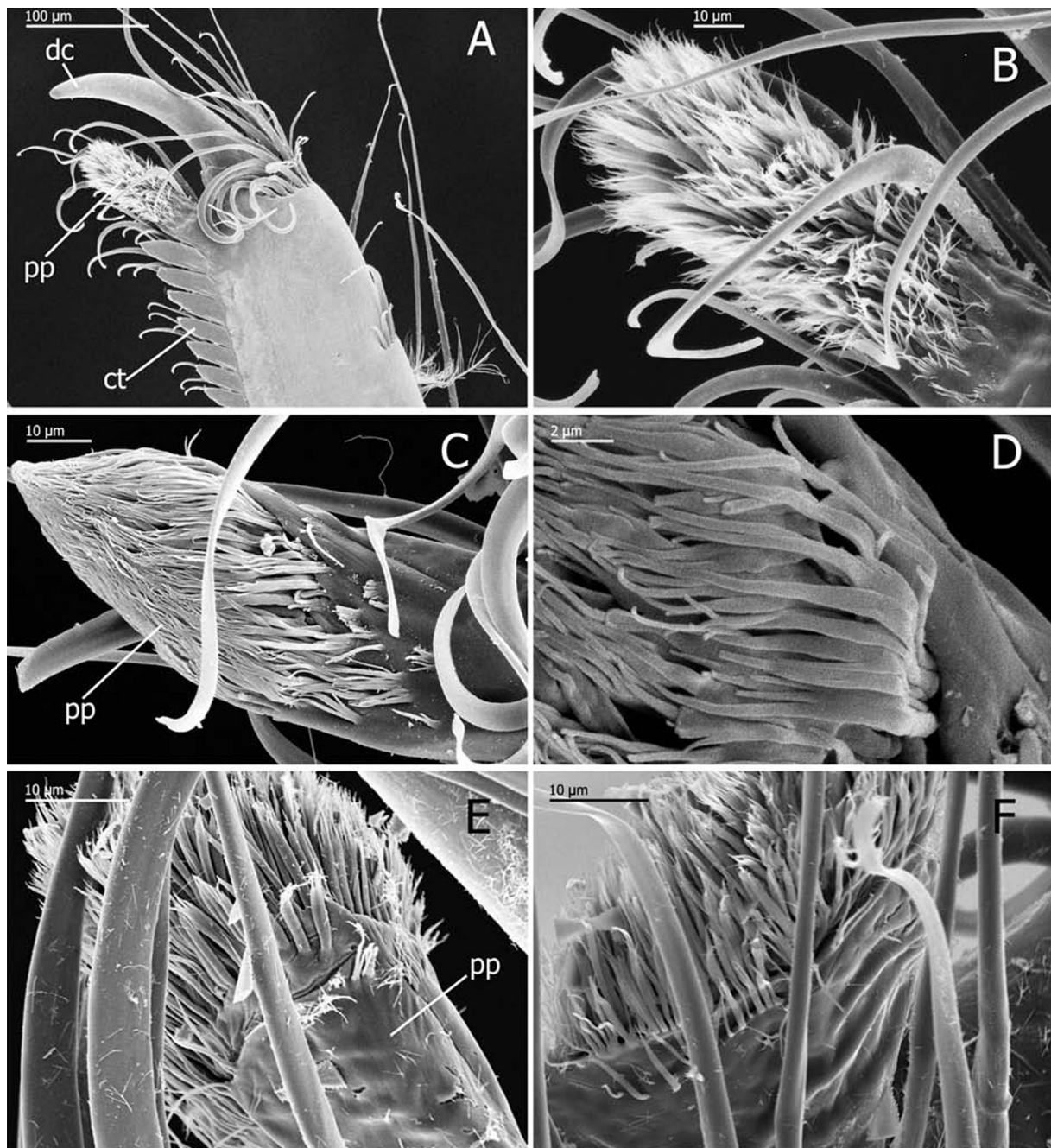


Figure 3. SEM micrographs of distal region of dactyl of right fourth pereopod and preungual process in *Phimochirus holthuisi* (Provenzano, 1961) (USNM): A, distal region of dactyl (mesial view); B, preungual process of same; C, preungual process in another specimen Mesial view); D, flat, seta-like filaments of same; E, distal region of preungual process in another specimen (mesial view; filaments in foreground not part of preungual process); F, distal region of preungual process of same in slightly higher magnification. Abbreviations as in Fig. 1.

short, stout tubular projection with a dense brush distally (Fig. 5). The brush has two types of seta-like filaments: 1) thin and flat, located on the distal half; and 2) short and tubular, forming a patch proximally, each filament having a terminal opening that suggests the presence of a lumen.

SEM micrographs of a specimen of an undetermined species of *Enallopagurus*, reveal a preungual process quite different than that described above for *E. spinicarpus* using light microscopy. In *Enallopagurus* sp., the process is club-like, reaching to about midlength of the dactylar claw, distally rounded and with short, thick seta-like filaments distally (Fig. 6A).

In *Lophopagurus* (*Lophopagurus*) *thompsoni* (Filhol, 1885), a species distributed around southern New Zealand, in the subtidal to 293 m (McLaughlin and Gunn, 1992), the preungual process (Fig. 6B) is prominent, extending slightly beyond the midlength of the dactylar claw, and terminating in a blunt point. The basal portion is naked, whereas distally there are what appear to be broken, seta-like filaments.

Discussion

Clearly, the present study has generated more questions than answers, but we now have a rea-

sonably detailed morphological assessment of the preungual process in three species of *Phimochirus* McLaughlin, 1981, and better insight than previously about this process in six other species in the Paguridae. Among the key questions that remain unanswered is the ontogenetic origin of the preungual process and its phylogenetic significance. Comparisons of the morphologies of the preungual processes in the species included in this study, as well as stereomicroscope observations of representatives from all other taxa of Paguridae reported to have preungual processes, reveal a wide range of complexity of this process, from a simple and often obscure protuberance as documented by McLaughlin (1974) for several species of *Pagurus*, to well developed and densely covered with seta-like filaments as documented by Asakura (2001, as *Catapagurus* and *Hemipagurus*) and McLaughlin (2004) in descriptions of *Catapagurus* species. In the Paguridae, the preungual process is located near the base of the dactylar claw on the lateroventral or mesioventral side, and usually close to the distal-most tooth that is part of the row of corneous teeth on the ventrolateral margin of the dactyl. It would appear, based on its location, that the preungual process might represent a modified tooth. However, it is also possible that it represents a specialized element of the dactyl. In the Diogeni-

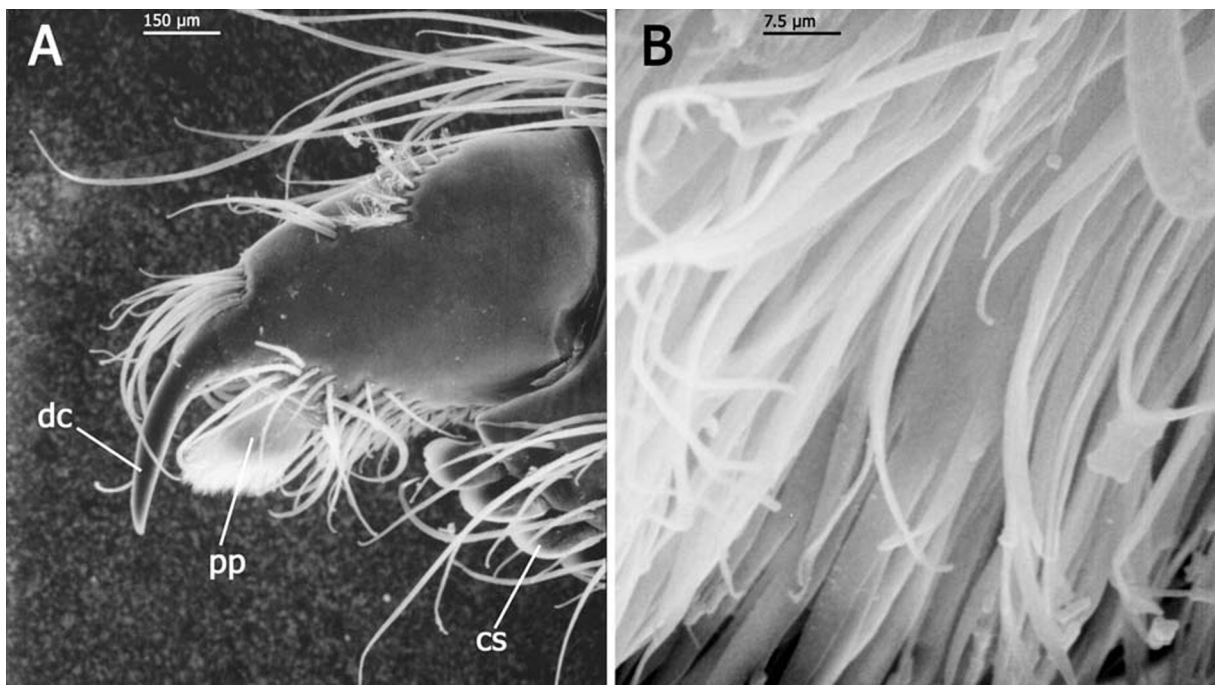


Figure 4. SEM micrographs of distal region of dactyl of right fourth pereopod and preungual process in *Phimochirus operculatus* (Stimpson, 1859) (RSMAS): A, distal region of dactyl (mesial view); B, magnified portion of region with flat, seta-like filaments of same. Abbreviations as in Fig. 1.

dae *Pseudopaguristes bicolor* Asakura and Kosuge, 2004 and *P. shidarai* Asakura, 2004, the preungual processes are drastically different than those found in species of the Paguridae. In these two diogenids, the process consists of a long, slender filament. In some species of the diogenid genera *Areopaguristes* Rahayu & McLaughlin, 2010 (formerly *Stratiotes* Thomson, 1899) and *Paguristes* Dana, 1851, the

preungual process appears to be inserted in the ventrolateral row of dactylar teeth (Komai, 2001, 2009) rather than under the dactylar claw as in the Paguridae. Thus, it would appear that the preungual processes in the Paguridae and Diogenidae are not necessarily homologous structures. Even within the Paguridae, the process can vary considerably in morphological complexity and degree of devel-

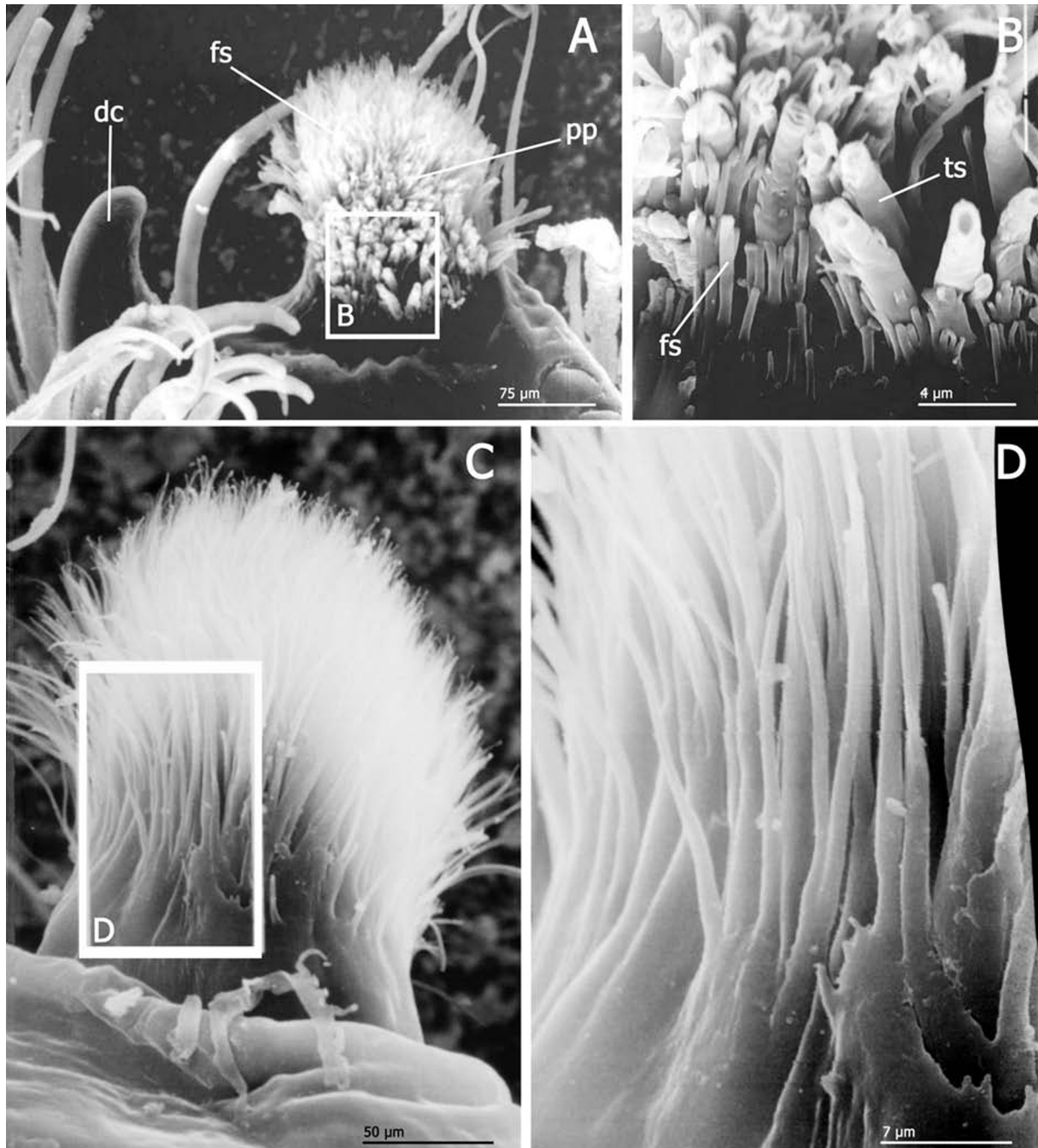


Figure 5. SEM micrographs of distal region of dactyl of left fourth pereopod and preungual process in *Phimochirus randalli* (Provenzano, 1961) (RSMAS): A, distal region of dactyl (ventral view); B, region of preungual process indicated as inset in A, showing seta-like filaments; C, preungual process in another specimen; D, region of preungual process indicated as inset in C, showing seta-like filaments. Abbreviations as in Fig. 1, except for fs, flat seta-like filament, and ts, tubular seta-like filament.

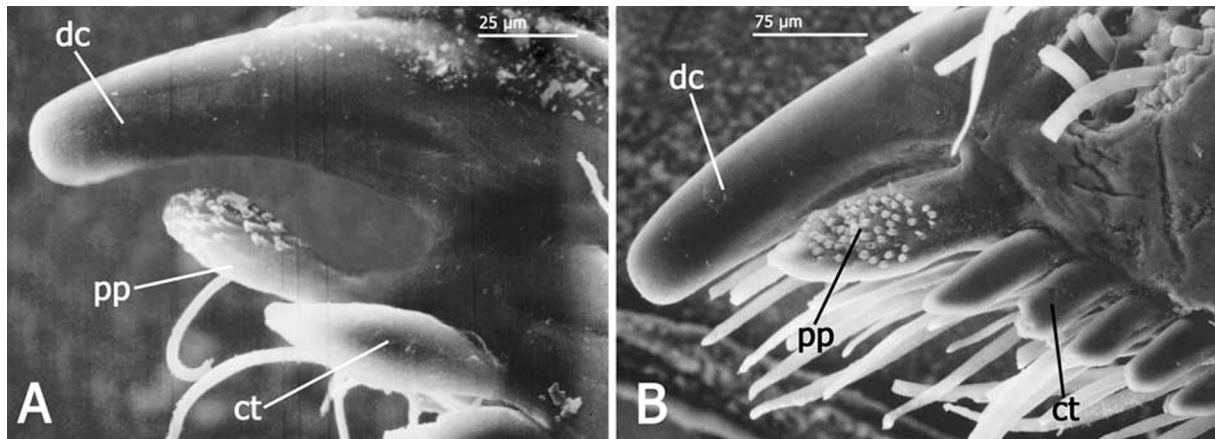


Figure 6. SEM micrographs of distal region of dactyl of right fourth pereopod and preungual process (RSMAS): A, *Enallopagurus* sp. (mesial view); B, *Lophopagurus* (*Lophopagurus*) *thompsoni* (Filhol, 1885) (mesial view). Abbreviations as in Fig. 1.

opment depending on species, genera, and family, and thus homology is also questionable within species of this family.

Studies on hermit crab behavior that have focused on the crab-gastropod shell association have assumed that morphological specialization of the fourth pereopods such as the propodal rasp, is an adaptation related to shell use (e.g., Hazlett, 1981; Dunham, 1983; Scully, 1983). That the majority of hermit crabs species that so far have been found to have a preungual process utilize gastropods shells for shelter, might suggest a sensory function of this process that is related also to shell selection and manipulation. However, not all species that have a preungual process live in gastropod shells, and thus the factors that have influenced development of this process, and its function, may be varied. The species used in this study are known to use gastropod shells as shelter, except for *Lophopagurus* (*L.*) *thompsoni*, which lives symbiotically with bryozoans (Forest and McLay, 2001). Also, juveniles of *Catapagurus sharreri* have been reported to use scaphopod or pteropod shells where anemones settle, and adults are known to use gastropod shells covered by polyps of coelenterates such as the actinian *Adamsia sociabilis* Verrill, 1883 or the zoanthid *Epizoanthus incrustatus* von Dübén and Koren, 1847, that form carcinoecia (Verrill, 1883; Agassiz, 1888; Balss, 1924). Other species of *Catapagurus* and *Catapaguropsis* Lemaitre and McLaughlin, 2006 that are frequently found living in small shells associated with some anemone, also have prominent and well developed preungual processes (Asakura, 2001; McLaughlin, 2004; McLaughlin

and Lemaitre, 2007), although this association is probably not obligatory or universal. The shells are usually small, and although the coelenterates add size to the carcinoecium, the reduced pleon of the hermit crab is not covered entirely. Adding to the puzzling questions on the possible function of the preungual process is that a number of hermit crabs such as species of *Anapagurus* Henderson, 1886, of the Paguridae, and various species of Parapaguridae, are well known for their associations with various coelenterates yet do not have a preungual process (García-Gómez, 1994; Lemaitre, 1989, 1999, 2004; Ates, 2003). Whether habitat or other environmental factors influence development and variability of the preungual process in these species is yet to be explored. Experiments with live specimens and more detailed morphological and histological studies are needed to fully comprehend the complexity, function and evolutionary significance of the preungual process in the Paguroidea.

Acknowledgements

We thank the late Gilbert L. Voss, and Nancy Voss, for allowing use of the RSMAS invertebrate collections. At FIU, we thank George Taylor for providing access to the SEM lab facilities. At USNM we are grateful to the SEM lab manager, Scott Whittaker, for guidance and assistance; Sarah Trunnell enthusiastically prepared many specimens and took micrographs as part of an internship project; Bill Moser and Rose Gullede helped with preparing images. Part of this paper was presented during the Biology of Anomura III Symposium held at The Crustacean Society's 2009 annual meetings in Tokyo, Japan.

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Submitted 07 December 2009

Accepted 05 May 2010