Sistemática e historia evolutiva de la Familia Galatheidae (Crustacea: Anomura) en el Pacífico Sur

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Sistemática e historia evolutiva de la familia Galatheidae (Crustacea: Anomura) en el Pacífico Sur

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Para Fer,
magnífico compañero de trabajo y mejor amigo

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INDICE

Resumen

El presente trabajo se ha centrado en los decápodos anomuros de la familia Galatheidae Samouelle, 1819, que incluyen alrededor de 700 especies principalmente asociadas a aguas profundas (>200 m) y distribuidas en todos los hábitats marinos del mundo. Aproximadamente el 80% de las especies del grupo se concentran en la región Suroeste del Pacífico, con un pico máximo de diversidad en la región de Nueva Caledonia y aguas adyacentes. A pesar de que la taxonomía de la familia se considera razonablemente estable, nuevos géneros y especies son descritos anualmente, por lo que parece que aún se está lejos de conocer su diversidad real. Los representantes de esta familia, tanto por su distribución como por su diversidad, proporcionan una oportunidad excelente para abordar el estudio de la diversificación, la biogeografía y, en general, los procesos evolutivos generadores de diversidad en la región del Pacífico. Por lo tanto, los principales objetivos de esta Tesis Doctoral fueron realizar una revisión de la sistemática de distintos géneros de la familia Galatheidae, evaluando la utilidad tanto de caracteres morfológicos así como la de distintos marcadores moleculares (mitocondriales y nucleares), y establecer un marco taxonómico, filogenético y biogeográfico robusto para interpretar su historia evolutiva.

El estudio morfológico llevado a cabo ha revelado la variedad de caracteres diagnósticos existentes para ordenar la diversidad biológica dentro la familia Galatheidae. Asimismo, se ha destacado el valor taxonómico de sutiles diferencias morfológicas así como la necesidad de revisar la validez de algunas de ellas, especialmente en los géneros *Agononida* Baba y de Saint Laurent, 1996, *Munida* Leach, 1820 y *Allogalathea* Baba, 1969. Los marcadores mitocondriales seleccionados resultaron útiles para detectar diferencias genéticas a nivel de género y especie; sin embargo, no todos los genes nucleares fueron idóneos para identificar esa variabilidad. El estudio conjunto de caracteres morfológicos y moleculares permitió detectar la existencia de varias especies crípticas, habiéndose descrito un nuevo género y un total de 22 nuevas especies para la Ciencia. Las filogenias moleculares inferidas a partir de genes mitocondriales no pudieron resolver las relaciones evolutivas a nivel intra e intergenérico. Aunque la incorporación de genes nucleares mejoró la resolución, tampoco pudieron resolver completamente las relaciones. Este

resultado sugiere que la falta de soporte en los nodos más basales podría estar relacionada con un modo de especiación explosivo más que con una falta de caracteres informativos o saturación de los marcadores seleccionados.

Con el objetivo de testar dicha hipótesis se analizó la filogenia molecular del género *Paramunida* Baba, 1988, estableciendo una escala espacio-temporal para el origen y diversificación del grupo así como una propuesta biogeográfica de reconstrucción de áreas ancestrales. Las estimas de los tiempos de divergencia utilizando una aproximación de reloj molecular relajado, indicaron que la diversificación del género debió de acontecer durante el período comprendido entre el Oligoceno y el Mioceno. Distintos análisis apoyaron la existencia de un evento de rápida especiación así como una aceleración en las tasas de diversificación durante ese período, seguido de una disminución en las tasas de acumulación de linajes. La intensa actividad tectónica de esa época en la región Pacífica, así como los cambios acontecidos en el régimen de temperatura global y corrientes oceánicas generaron nuevos hábitats, lo que debió de de promover la diversificación de la fauna marina tanto en aguas superficiales como profundas. Una primera aproximación a su historia biogeográfica propone la región del Pacífico Suroeste como centro de especiación del grupo y destaca el hecho de que la distancia geográfica no parece representar una barrera al flujo génico, siendo probablemente otros factores como retención larvaria, corrientes oceánicas u orografía marina más determinantes. Futuras investigaciones incluyendo un mayor número de taxones así como un mayor número de datos morfológicos y moleculares, nos permitirán mejorar el conocimiento de la evolución de los caracteres morfológicos y la propuesta de inferencias filogenéticas más robustas sobre las que seguir explorando el origen y diversificación de la familia.

Los resultados de la presente Tesis Doctoral se muestran estructurados en los siguientes capítulos:

Capítulo I.
Cabezas P, Macpherson E, Machordom A. 2008. A new genus of squat lobster (Decapoda: Anomura: Galatheidae) from the South West Pacific and Indian Ocean inferred from morphological and molecular evidence. *Journal of Crustacean Biology* **28:** 68-75.

Capítulo II.

Cabezas P, Macpherson E, Machordom A. 2009**.** Morphological and molecular description of new species of squat lobster (Crustacea: Decapoda: Galatheidae) from the Solomon and Fiji Islands (South-West Pacific). *Zoological Journal of the Linnean Society* **156:** 465-493.

Capítulo III.
Cabezas P, Macpherson E, Machordom A. 2010. *Allogalathea* (Decapoda: Galatheidae): a monospecific genus of squat lobsters?. *Zoological Journal of the Linnean Society* (aceptado).

Capítulo IV.
Cabezas P, Macpherson E, Machordom A. 2010. Taxonomic revision of the genus *Paramunida* Baba, 1988 (Decapoda: Galatheidae): a morphological and molecular approach. *Zootaxa* (enviado).

Capítulo V.
Cabezas P, Sanmartín I, Paulay G, Macpherson E, Machordom A. 2010. Deep under the sea: Unraveling the evolutionary history of the deep-sea squat lobster *Paramunida* (Decapoda, Galatheidae) (por enviar).

Asimismo, durante el desarrollo de este trabajo se pudieron abordar y publicar los resultados relacionados con una revisión taxonómica de las familias Chirostylidae, Galatheidae y Kiwaidae, así como el desarrollo de un genoteca para una especie de galateido en peligro de extinción (Anexos I y II):

Anexo I.
Baba K, Macpherson E, Poore GCB, Ahyong ST, Bermudez A, Cabezas P, Lin CW, Nizinski M, Rodrigues C, Schnabel KE. 2008. Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura - families Chirostylidae, Galatheidae and Kiwaidae). *Zootaxa* **1905:** 1-220.

Anexo II.
Cabezas P, Bloor P, Acevedo I, Toledo C, Calvo M, Macpherson E, Machordom A. 2009. Development and characterization of microsatellite markers for the endangered anchialine squat lobster *Munidopsis polymorpha*. *Conservation Genetics* **10:** 673-676.

Introducción general

En la presente memoria se ha abordado el estudio de la historia evolutiva de la familia Galatheidae Samouelle, 1819 desde una aproximación morfológica, molecular y biogeográfica. Con el objetivo de contextualizar los diferentes capítulos, a continuación se aporta una revisión de los últimos avances y herramientas aplicadas a los campos de la sistemática y la biogeografía, así como una visión general de los principales aspectos del grupo objeto de estudio.

El descubrimiento de una nueva especie está entre los logros más importantes que un biólogo puede llevar a cabo (Wilson, 1998). Las especies son la unidad básica de estudio en muchos campos de la biología, por lo que una correcta identificación y clasificación de las mismas es esencial. La rama de la biología encargada de ordenar la diversidad biológica es la sistemática, dividida a su vez en dos campos, la taxonomía y la filogenia. Por un lado la taxonomía se encarga de descubrir, identificar, describir, nombrar y clasificar los taxones, mientras que la filogenia estudia la historia evolutiva y las relaciones entre organismos (Wiens, 2007).

Taxonomía

Durante siglos la taxonomía representó una de las disciplinas más importantes dentro de la biología. Sin embargo, en las últimas décadas ha sufrido un importante declive y muchos grupos taxonómicos adolecen de la falta de especialistas que los estudien. La biodiversidad, que incluye el conjunto de toda la vida en nuestro planeta en cualquiera de sus niveles, desde genes a ecosistemas, garantiza en su conjunto el correcto funcionamiento de la biosfera, regulando todos los ciclos y proporcionando una insustituible fuente de recursos primarios.

Actualmente estamos asistiendo a un crisis de biodiversidad global, y las continuas y severas perturbaciones del medio natural están precipitando la extinción de un gran número de especies (Brook *et al.*, 2006). En ese sentido, la extinción es un proceso irreparable, y supone la pérdida de linajes completos con millones de años de evolución. Dado que se asume la existencia de un gran número de especies no descritas (mayor incluso que el número total de especies conocidas a día de hoy), la catalogación de la diversidad biológica debería ser considerada una demanda social de

primer orden (Bickford *et al.*, 2007), tanto por su valor puramente informativo, como por su directa relación con la conservación y manejo de nuestros recursos naturales.

La ordenación de tan rica diversidad requiere establecer unos límites y criterios para poder definir qué se considera una especie. El proceso por el cual se establecen esos límites para finalmente poder determinar el rango taxonómico de especie se ha convertido en uno de los temas más discutidos en la sistemática moderna (Sites Jr y Marshall, 2004; Wiens, 2007). El advenimiento de nuevas metodologías para explorar esos límites ha acelerado la tasa a la cual nuevas especies son descubiertas y descritas (Mishler y Donoghue, 1982; Hebert *et al.*, 2004), reactivando a su vez un debate histórico como es el concepto de especie (Tautz *et al.*, 2003; Wheeler, 2004). El establecimiento de los límites de especies está claramente supeditado al concepto de especie que apliquemos a nuestro estudio (de Queiroz, 1998), y aunque los conceptos biológico, ecológico, evolutivo y filogenético son los más familiares, existen otros muchos basados en distintos criterios y metodologías (Tabla 1). Tal disparidad refleja los intereses específicos de cada disciplina de la biología. De este modo, el criterio de barrera reproductiva es fundamental para aquellos estudios de zonas híbridas, la ocupación de distintos nichos para la ecología, las diferencias morfológicas son la clave para los taxónomos clásicos, así como las moleculares lo son para los genetistas y la existencia de grupos monofiléticos es el criterio a seguir en estudios filogenéticos (de Queiroz, 2007).

Durante años se ha buscado crear un concepto unificado de especie, centrándose en las similaridades de los distintos criterios en lugar de sus disparidades. La propuesta más reciente traslada la conceptualización del término de especie a la conceptualización del término metapoblación (de Queiroz, 2007). De este modo se define especie como un segmento de un linaje que evoluciona de manera independiente a lo largo del tiempo (metapoblación), considerando la monofilia o el aislamiento reproductivo como características secundarias de las especies que pueden ser o no ser adquiridas a lo largo del proceso evolutivo. En otras palabras, una metapoblación para ser considerada especie no tiene porqué ser monofilética, representar aislamiento reproductivo, ser ecológicamente divergente y morfológicamente distinguible, sino que la sola existencia de uno de esos atributos

puede considerarse suficiente evidencia de la separación de linajes. A día de hoy esa propuesta representa uno de los mayores esfuerzos que se ha realizado por intentar unificar conceptos; no obstante, añade aún más complejidad al problema con la introducción del término metapoblación, por lo que la búsqueda de un concepto unificado de especie continúa siendo un debate abierto (Baum, 2009).

Tabla 1. Distintos conceptos de especie y criterios empleados para su delimitación (adaptado de Queiroz, 2007).

Concepto de especie	Criterio	Referencias
Biológico	Cruzamiento (reproducción exitosa con viabilidad y fertilidad de la descendencia)	a
Aislamiento	Aislamiento reproductivo intrínseco (ausencia de cruzamiento entre organismos heteroespecíficos, no generado por barreras geográficos)	b
Reconocimiento	Reconocimiento específico de pareja y sistema de fertilización	c
Ecológico	Mismo nicho ecológico o zona adaptativa (incluye todos los componentes del ambiente en el cual actúan los organismos)	d
Evolutivo	Historia evolutiva compartida	e
Cohesión	Cohesión fenotípica (intercambio genético o geográfico)	f
Filogenético		
Hennigniano	El ancestro se extingue cuando dos linajes se separan	g
Monofilético	Monofilia. Se incluye el ancestro y todos sus descendientes. Caracteres derivados compartidos	h
Genealógico	Coalescencia. Todos los alelos de un gen descienden de un alelo común no compartido con otras especies	i
Diagnosticable	Criterio cualitativo. Diferencias fijadas.	j
Fenético	Agrupación de clados fenéticos. Diferencias cuantitativas	k
Grupo genotípico	Agrupación de genotipos (p.e. falta de heterozigotos)	l

a) Wright (1940); Mayr (1942); Dobzhansky (1950); **b)** Mayr (1942); Dobzhansky (1970); **c)** Paterson (1985); Masters *et al.*, (1987); Lambert y Spencer (1995); **d)** Van Valen (1976); Andersson (1990); **e)** Simpson (1951); Wiley (1978); Mayden (1997); **f)** Templeton (1998, 1998a); **g)** Hennig (1966); Ridley (1989); Meier y Wilmann (2000); **h)** Rosen (1979); Donoghue (1985); Mishler (1985); **i)** Baum y Shaw (1995), Avise y Ball (1990); **j)** Nelson y Platnick (1981); Cracraft (1983); Nixon y Wheeler (1990); **k)** Michener (1970); Sokal y Crovello (1970); Sneath y Sokal (1973); **l)** Mallet (1995) (referencias citadas en de Queiroz, 2007).

En la presente Tesis se aporta la descripción de un género y un total de 22 especies nuevas para la Ciencia. La falta de conocimiento acerca de muchos aspectos de la biología y ecología de las especies estudiadas hace imposible la utilización de un criterio ecológico o biológico de especie. Por lo tanto, ya que principalmente la propuesta de nuevas especies se realizó en base a criterios morfológicos (adultos y larvarios) y moleculares, consideramos que lo más correcto es basarnos en un criterio fenético y filogenético (monofilia). En algunos casos, los nuevos taxones descritos se caracterizan por presentar diferencias morfológicas sutiles con sus especies hermanas en contraste con unas grandes divergencias genéticas. Este fenómeno por el cual el proceso de cladogénesis no está asociado a cambio morfológico es lo que se conoce como especiación críptica.

Consideramos que dos o más especies son crípticas si son o fueron clasificadas como una única especie nominal debido a la aparente falta de diferencias morfológicas. La existencia de estas especies ha sido reconocida desde hace más de 300 años, pero su descripción se ha incrementado exponencialmente desde la introducción de herramientas moleculares en estudios taxonómicos (Agapow *et al.*, 2004; Bickford *et al.*, 2007). Históricamente, las relaciones filogenéticas dentro del reino animal han sido abordadas desde un punto de vista morfológico (Giribet *et al.*, 2007), pero aunque nuevas técnicas como la microscopía electrónica de barrido permiten estudiar con una mayor precisión los caracteres morfológicos, la aplicación de técnicas moleculares es lo que ha transformado de manera decisiva nuestra habilidad para describir y clasificar la diversidad biológica.

Esta revolución aunque presenta un gran número de ventajas (Tautz *et al.*, 2003; Blaxter, 2004), plantea nuevos y desafiantes retos para la taxonomía. Actualmente, una primera fase de obtención de datos moleculares requiere una menor inversión de tiempo que un estudio de los caracteres morfológicos. De este modo, multitud de estudios biogeográficos o evolutivos basados en el análisis de secuencias de ADN con objetivos eminentemente no taxonómicos, plantean ahora el problema de cómo actuar ante el descubrimiento de nuevos taxones (Padial y de la Riva, 2007). Claramente las herramientas moleculares presentan la ventaja de que un gran número de investigadores pueden aportar nuevas y valiosas contribuciones al

campo de la taxonomía, y su potencial en combinación con otro tipo de información (ecológica, morfológica, biológica…) parece indiscutible. No obstante, supone a su vez una gran desventaja puesto que el tiempo que una persona en período de formación debería dedicar a conocer las características biológicas básicas de los organismos se ve drásticamente reducido.

Muchas son las críticas que ha recibido la taxonomía del ADN, principalmente por parte de aquellos investigadores que defienden una taxonomía clásica basada estrictamente en criterios morfológicos (Valdecasas *et al.*, 2007). Sin embargo, algunas de esas críticas parecen asumir implícitamente que la delimitación de especies con caracteres morfológicos es infalible y sencilla, cuando indudablemente está sometida al criterio no exento de error del taxónomo (Wiens, 2007). Una especie puede ser descrita sólo en base a caracteres morfológicos y eso es considerado suficiente evidencia (Macpherson, 2009; Hidalgo-Galiana *et al.*, 2010). No obstante, la combinación de esos caracteres con una fuente adicional de información, como análisis filogenéticos de secuencias de ADN o datos ecológicos, puede aportar una mayor robustez y veracidad al nuevo estatus taxonómico de esas especies (de Queiroz, 2007). Por tanto, el debate no es si es más adecuado un criterio basado en secuencias de ADN o en caracteres morfológicos, sino el hecho de basarse en una única fuente de información, ya sea morfológica o molecular (DeSalle, 2006).

Recientemente se ha acuñado el término taxonomía integradora, con el objetivo de definir una taxonomía pluralista basada en el empleo de distintas líneas de evidencia para la descripción de especies (Dayrat, 2005; Will *et al.*, 2005). Asumiendo que el último fin de un biólogo evolutivo es comprender el proceso evolutivo, si existe la posibilidad de evaluar el estatus de una nueva especie desde distintos puntos de vista sería imprudente no hacerlo. La frecuencia con la cual nuevas especies están siendo descubiertas gracias a la incorporación de secuencias de ADN, sugiere que las herramientas moleculares deberían ir siendo incorporadas de manera progresiva a la rutina de los estudios de alfa taxonomía, siendo muy recomendable la conservación de material fresco de los ejemplares para su posible análisis molecular. De esta forma, una taxonomía basada en criterios estrictamente morfológicos como estrictamente

moleculares tiene sus limitaciones, revelándose la combinación de ambas fuentes de información como la mejor estrategia para realizar estudios en sistemática.

Filogenia

Como ya ha sido comentado, la filogenia se encarga de interpretar las relaciones entre taxa con el fin de determinar cómo sucedió su diversificación (Wiens, 2007). Los organismos evolucionan a través del tiempo desde formas ancestrales a formas derivadas, originándose nuevas especies que retienen características de sus ancestros, las cuales son modificadas y suplementadas con nuevos caracteres. Los diferentes clados de una filogenia se caracterizan por la posesión de caracteres derivados compartidos (sinapomorfías), que son aquellos caracteres que nos van a permitir definir grupos monofiléticos y, en nuestro caso, poder determinar la existencia de nuevas especies.

El desarrollo de técnicas de amplificación de ADN en trabajos de sistemática permite incluir un gran número de caracteres para resolver las relaciones filogéneticas entre organismos. Este hecho es de particular importancia en grupos donde los caracteres morfológicos presentan un alto grado de homoplasia y, por tanto, es complicado establecer homologías (Glenner *et al.*, 2003; Pérez-Losada *et al.*, 2009). Sin embargo, los caracteres moleculares también acusan este problema, puesto que múltiples sustituciones en una posición en particular y la inserción o deleción de segmentos de un gen pueden derivar también en fenómenos de homoplasia.

La homología de los caracteres moleculares es incorporada en los análisis filogenéticos a través del alineamiento de secuencias. Durante esa fase se pretende establecer qué posiciones proceden de un carácter ancestral común y por tanto son indicadoras de relaciones evolutivas entre secuencias. La estrategia más recomendable es llevar a cabo distintos alineamientos con el objetivo de identificar aquellas regiones en las que es difícil determinar la homología de los caracteres con precisión (Talavera y Castresana, 2007). El siguiente paso consiste en realizar análisis independientes incluyendo y excluyendo esas regiones con el objetivo de evaluar su grado de incertidumbre. En la actualidad, hay un gran número de paquetes informáticos que permiten realizar esta labor bajo distintos algoritmos matemáticos (Castresana, 2000;

Edgar, 2004). Sin embargo, todos ellos están sujetos a error por lo que siempre es aconsejable realizar una última correción manual. Los alineamientos de secuencias de ADN representan uno de los talones de Aquiles de la sistemática molecular actual, y aunque no es posible garantizar un 100% de homología, el empleo de distintas estrategias de alineamiento junto con el estudio de distintos marcadores moleculares puede proporcionar un marco robusto para inferir relaciones evolutivas.

Diferentes genes o regiones nucleotídicas evolucionan a distintas tasas y además los cambios dentro de cada uno de ellos no suceden totalmente de forma aleatoria, sino que algunas posiciones pueden ser invariables mientras que otras pueden acumular un gran número de mutaciones (Frank y Lobry, 1999). Los modelos de sustitución nucleotídica que intentan reflejar estos hechos incluyen los parámetros de frecuencia de bases, probabilidad de cambio de una base a otra y variación de las tasas de sustitución en cada una de las posiciones (Figura 1) (Posada y Crandall, 1998). La frecuencia de bases describe la proporción de cada uno de los nucleótidos sobre la longitud total de la secuencia. La tasa de cambio entre bases estima la tendencia de sustitución de unas a otras, siendo teóricamente más probables las transiciones que las transversiones. Por último, la tasa de variación en cada uno de los sitios puede ser diferente; de hecho, si la mayoría de posiciones de una secuencia evolucionaran lentamente o fueran invariables, entonces la tasa de cambio tendería a acumularse en unas pocas posiciones dando como resultado la saturación de esas posiciones (Palero y Crandall, 2009). Estos dos últimos aspectos (posiciones invariables y tasa de cambio de cada nucleótido) se estiman a través de los parámetros γ e I y complementan los siguientes modelos:

-Jukes-Cantor (JC) (Jukes y Cantor, 1969): se trata del modelo más simple y asume que la frecuencia de bases es idéntica y que todas las sustituciones son igualmente probables.

-Kimura 1980 (K80) o Kimura 2 parámetros (K2P) (Kimura, 1980): las frecuencias de las bases son idénticas, pero en este caso la probabilidad de que suceda una transición es mayor que la de una transversión.

-Felsenstein 1981 (F81) (Felsenstein, 1981): en este modelo se asume que la frecuencia de bases es diferente y que todas las sustituciones son igualmente probables.

-Hasegawa, Kishino y Yano 1985 (HKY85) (Hasegawa *et al.*, 1985): este modelo es una combinación de los dos modelos anteriores puesto que asume distinta frecuencia de bases y una probabilidad diferencial para las transiciones y transversiones.

-Modelo General Reversible (REV) (Rodríguez *et al.*, 1990): se trata del modelo más complejo y asume distinta frecuencia de bases y un total de seis tasas de sustitución diferentes entre los nucleótidos adenina, timina, guanina y citosina.

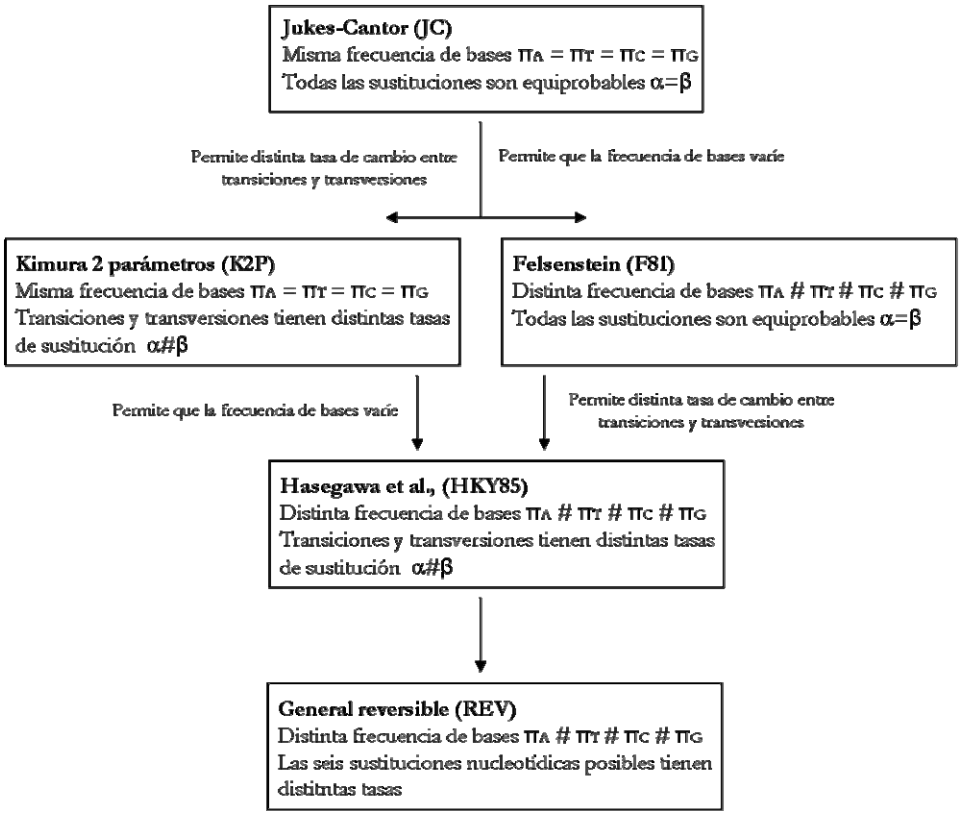


Figura 1. Relación de los cinco principales modelos para estimar el número de sustituciones nucleotídicas entre pares de secuencias de ADN. Los modelos JC, K2P, F81 y HKY85 pueden ser generados introduciendo restricciones sobre el modelo REV.

La tarea fundamental de las filogenias moleculares es convertir la información de secuencias de ADN en un árbol evolutivo que refleje las relaciones entre dichas secuencias. Los distintos métodos de inferencia filogenética pueden dividirse siguiendo dos criterios, por un lado cómo se manejan los datos y por el otro teniendo en cuenta la metodología que siguen para reconstruir topologías.

Los principales métodos de inferencia filogenética son máxima verosimilitud (ML), inferencia Bayesiana (BI), máxima parsimonia (MP) y métodos de distancia. En primer lugar se puede hacer una división mayor entre los métodos de distancia y el resto, puesto que son los únicos que convierten los datos en una matriz de distancia o divergencias, mientras que los otros trabajan con caracteres discretos considerando por separado cada una de las posiciones del alineamiento. En segundo lugar se pueden diferenciar los métodos de agrupamiento (NJ) y los de búsqueda (MP, ML, BI). El primero utiliza un algoritmo para obtener un árbol, mientras que los métodos de búsqueda emplean un criterio de optimización que permite asignar a cada árbol un valor, de manera que se puedan testar hipótesis alternativas y estimar el grado de ajuste entre las topologías obtenidas y los datos observados. Por último, la gran diferencia radica en el hecho de poder o no implementar modelos de evolución nucleotídica; de este modo los métodos de NJ, ML y BI lo permiten, mientras que la MP no puede hacerlo.

Máxima verosimilitud

Los métodos basados en máxima verosimilitud consideran la inferencia filogenética como un problema estadístico. Esta metodología calcula la probabilidad de observar los datos (alineamiento de secuencias) dado un árbol filogenético (topología) y un modelo evolutivo de secuencias (Felsenstein, 1981; Hasegawa *et al.*, 1985). Por tanto queremos encontrar la probabilidad de obtener las secuencias observadas dado un árbol en particular.

Para calcular la verosimilitud de un árbol es necesario calcular la probabilidad, en cada posición del alineamiento, del estado observado dadas todas las posibles combinaciones de estados ancestrales. La probabilidad total a lo largo de la secuencia es el resultado del producto de todas las probabilidades en cada una de las

posiciones, repitiéndose este proceso para todas las posibles topologías, y eligiéndose aquella con una longitud de rama que maximiza la probabilidad de obtener los datos observados.

Los métodos basados en ML son más precisos y proporcionan inferencias filogenéticas más robustas que los métodos de parsimonia, ya que permiten incorporar modelos de evolución nucleotídica y testar estadísticamente una hipótesis. Sin embargo, el análisis depende de un modelo evolutivo, lo que puede conllevar interpretaciones filogenéticas erróneas si su elección no es correcta. Por lo general, los modelos más complejos son los que mejor se ajustan a los datos, aunque el mayor número de parámetros que manejan conlleva un aumento de la varianza en cada una de las estimas (Rodríguez *et al.*, 1990). Diferentes paquetes informáticos permiten estimar el modelo de evolución nucleotídica que mejor se ajusta a nuestros datos (Posada y Crandall, 1998; Nylander *et al.*, 2004), desarrollándose cada día modelos más complejos que se espera proporcionen nuevas ideas sobre el proceso de evolución molecular (Porter *et al.*, 2007). Por otro lado, los primeros algoritmos basados en ML requerían tiempos computacionales muy grandes, haciendo impracticables su estima cuando se trabajaba con un conjunto de datos con cientos o miles de secuencias; sin embargo, multitud de algoritmos de reciente aplicación permiten incorporar un mayor número de secuencias con tiempos computacionales razonables (p.e. PHYML (Guindon y Gascuel, 2003); GARLI (Zwickl, 2006); RAXML (Stamatakis, 2006)).

Inferencia Bayesiana

Los métodos de inferencia Bayesiana se asemejan a los de máxima verosimilitud en el sentido que ambos pueden implementar la información procedente de los modelos de evolución nucleotídica. Sin embargo hay una serie de diferencias fundamentales entre ambos métodos.

El análisis bayesiano busca la topología que tiene la mayor probabilidad de ser correcta dado un modelo evolutivo y una matriz de datos, al contrario de los análisis de ML que maximizan la probabilidad de que nuestro árbol pueda generar los datos observados. El cálculo de la probabilidad posterior implica evaluar todos los posibles

árboles y para cada uno de ellos, explorar todas las posibles combinaciones de longitud de rama y parámetros del modelo. Dado que el número de combinaciones que puede alcanzarse es enorme, lo que se realiza es una aproximación a esa probabilidad mediante el método conocido como Cadenas de Markov-Monte Carlo (MCMC) (Ronquist y Huelsenbeck, 2003).

El proceso parte de un árbol inicial, ya sea aleatorio o especificado *a priori*, con unas determinadas longitudes de rama y parámetros definidos por el modelo evolutivo. En el siguiente paso se propone un nuevo árbol con una modificación aleatoria de los parámetros y se compara la probabilidad posterior de esta topología con la del estado inicial. Si la probabilidad de que nuestros datos hayan generado esa topología es mayor o al menos no significativamente menor, que la del árbol inicial, aceptamos el nuevo estado y sobre éste generamos una nueva variación de los parámetros. Este proceso puede repetirse millones de veces hasta que el análisis alcanza una región del espacio muestral donde la combinación de topologías y parámetros presentan los mayores valores de probabilidad posterior, de modo que cuando la búsqueda de MCMC alcanza un equilibrio, la probabilidad de los árboles obtenidos es constante (fase de convergencia). Este análisis nos va a proporcionar una estima de la probabilidad de que la topología obtenida sea el verdadero árbol evolutivo dado los datos observados.

Con el objetivo de evitar que la búsqueda del árbol pueda quedar atrapada en un espacio de árboles subóptimos, es recomendable correr varias cadenas independientes desde el mismo punto de inicio. Por lo general se va a tener una cadena fría en la cual se va acumulando el árbol con el mejor valor de probabilidad posterior, mientras que las cadenas calientes son aquellas en las que se van a generar propuestas alternativas en base cambios aleatorios de los parámetros. Esto nos permite evaluar la robustez de nuestros datos, puesto que los distintos análisis deberían converger en propuestas filogenéticas similares. La falta de convergencia en estos análisis puede mostrar una falta de congruencia entre los datos empleados o la falta de suficientes caracteres informativos, lo que conllevaría estimas incorrectas de la topología del árbol.

Máxima parsimonia

Este método se basa en la idea de que la mejor hipótesis para explicar un proceso es aquella que requiere el menor número de pasos, por lo que ante dos posibles explicaciones válidas para un fenómeno, siempre es preferida la más simple.

La parsimonia trata de buscar el árbol o conjunto de árboles que minimiza la cantidad de cambio evolutivo, es decir, la transformación de un carácter en otro (Farris *et al.*, 1970). La principal ventaja de este método es su rapidez y que permite trabajar con distintos tipos de datos (p.e. morfológicos y moleculares). La principal objeción a esta metodología es que no permite implementar modelos de evolución nucleotídica, por lo que produce resultados inconsistentes cuando las secuencias muestran saturación o las tasas evolutivas entre linajes son muy diferentes (Hillis *et al.*, 1996). Por otro lado presenta el problema de atracción de ramas largas que va a generar el agrupamiento artificial de aquellas ramas de la filogenia que han acumulado un mayor número de mutaciones (Page y Holmes, 1998). Filogenias con pocos taxones son más sensibles a esta fuente de error, puesto que especies que hayan acumulado un mayor número de mutaciones van a ser agrupadas artificialmente porque por azar es más probable que hayan adquirido el mismo carácter de manera independiente (homoplasia).

En parsimonia, el cálculo de la topología óptima requiere calcular la cantidad de cambios de estado de un carácter para un árbol dado y buscar todas las posibles topologías que minimizan esa longitud. Para la búsqueda del mejor árbol existen distintos procedimientos. El exhaustivo evalúa todos los árboles posibles garantizando que se encuentra el árbol óptimo. Sin embargo computacionalmente es muy costoso y está aproximadamente limitado a un número total de 12 taxones, donde el número de árboles a evaluar sería del orden de millones (Tabla 2).

Tabla 2. Posibles reconstrucciones filogenéticas bajo un método de búsqueda exhaustivo.

OTUs	Árboles enraizados	Árboles sin enraizar
2	1	1
3	3	1
4	15	3
5	105	15
6	954	105
7	10.395	954
8	135.135	10.395
9	2.027.025	135.135
10	34.349.425	2.027.025
11	$>654x10^{6}$	$>34x10^{6}$
15	$>213x10^{12}$	$>7x10^{12}$
20	$>8x10^{21}$	$>2x10^{20}$
50	$>6x10^{81}$	$>2x10^{76}$

Por otro lado está la búsqueda de "branch and bound", muy similar a la anterior pero con la diferencia de que cuando se examina un árbol que tiene una longitud que excede la longitud del árbol óptimo encontrado hasta ese momento no continúa la búsqueda, por tanto todos esos árboles subóptimos son descartados sin necesidad de evaluarlos uno por uno. Por último, el método heurístico busca la topología óptima sin evaluar todas las posibilidades, por lo que no se puede garantizar que el árbol encontrado sea el que contenga el menor número de pasos evolutivos. Sin embargo, mediante este procedimiento se pueden evaluar topologías alternativas dentro de todo el espacio muestral de posibles árboles en un tiempo computacional razonable. Para evitar que la búsqueda pueda quedarse en un máximo local, hay distintos métodos que permiten adicionar taxones e intercambiarlos en las distintas ramas, evaluando en cada caso la longitud del árbol y rechazando aquellos con un número de pasos mayor (p.e. "tree bisection and reconnection" (Swofford y Sullivan, 2003)).

Una estrategia para evaluar si nuestro análisis ha encontrado un árbol óptimo, es realizar varios análisis independientes con distintos árboles de partida para asegurarnos de que se alcanzan soluciones parecidas y que, por tanto, el espacio muestral de árboles ha sido razonablemente muestreado.

Métodos de distancia

Los métodos de distancia se basan en el cálculo de las diferencias entre secuencias. Para ello se construye una matriz que calcula la distancia entre cada par de secuencias, buscándose posteriormente un árbol que refleje las distancias observadas. El número de posiciones diferentes puede ser una subestimación de la distancia genética real, ya que algunas posiciones han podido sufrir multitud de sustituciones. Así, la distancia genética puede ser corregida en base a modelos de sustitución nucleotídica, al igual que métodos indicados anteriormente.

La principal desventaja de este método radica en la inevitable pérdida de información al transformar un alineamiento de secuencias en una simple matriz de distancias (Page y Holmes, 1998) ya que no se tiene en cuenta la evolución de cada una de las posiciones de manera independiente.

Se han propuesto distintos métodos para la reconstrucción de árboles filogenéticos en base a distancias genéticas:

1. Mínima evolución (ME). Este método emplea búsquedas heurísticas para reconstruir árboles a partir de distancias. El criterio de optimización selecciona el árbol que tiene la menor longitud de rama (Rzhetsky y Nei, 1992).

2. Neighbor-joining (NJ). Esta metodología trabaja agrupando pares de secuencias sucesivamente. Se construye una matriz de distancias modificada en la que la separación entre cada par de nodos se ajusta en base a la divergencia media del resto de los nodos. No asume una tasa de evolución constante a lo largo de todo el árbol, por lo que es un método de reconstrucción adecuado cuando sabemos que nuestros datos no han evolucionado en base a un reloj molecular estricto.

3. UPGMA. Es similar a la metodología de NJ pero los árboles generados son ultramétricos, ya que se asume una tasa de evolución constante.

En la actualidad los métodos basados en distancia son cada vez menos empleados para estimar relaciones filogenéticas; sin embargo, su utilización en combinación con otros métodos de inferencia pueden añadir mayor soporte y credibilidad a las reconstrucciones filogenéticas. Por otro lado, los valores de

divergencia basados en distancia son ampliamente utilizados en taxonomía para apoyar el estatus taxonómico de las especies y aunque algunos trabajos han intentando proponer un umbral para definir el límite de especie (Lefébure *et al.*, 2006), de manera habitual queda a criterio del taxónomo.

Medida de soporte de árboles

Los anteriores métodos descritos nos permiten realizar una estima de las relaciones filogenéticas de los organismos objeto de estudio, pero no nos proporcionan una medida del grado de confianza de dicha hipótesis.

Una propuesta filogenética poco soportada suele estar relacionada no con el método utilizado para la reconstrucción, sino con los datos empíricos. Esto puede suceder si los marcadores seleccionados no son adecuados para nuestro estudio, ya sea por falta o exceso de variablidad, problemas de saturación, presencia de pseudogenes… Si por el contrario, los genes empleados en el estudio se creen apropiados, una filogenia con poco apoyo estadístico puede apuntar hacia una falta de muestreo o una historia evolutiva marcada por rápidos procesos de cladogénesis.

El método más extendido para testar el grado de fiabilidad de una hipótesis filogenética es el bootstrap (Bv) (Felsenstein, 1985). Es una técnica de remuestreo que asume que los datos empíricos son representativos del universo al que representan (cada uno de los caracteres contiene la misma señal filogenética), y por tanto pueden generarse nuevas muestras por remuestreo aleatorio de la misma. Cada pseudorréplica se va a obtener mediante remuestreo con reemplazamiento de los datos originales, por lo que el porcentaje de pseudorréplicas que apoya la hipótesis es considerado una medida de confianza. Posteriormente se obtiene un árbol para cada una de las pseudorréplicas siendo el apoyo de una rama el porcentaje de veces que un mismo clado aparece en el conjunto de árboles de las pseudoréplicas. Esta metodología puede ser aplicada a los análisis basados en distancias genéticas, MP y ML, aceptándose como robustos valores de Bv iguales o superiores al 70%.

Por último, el apoyo de los distintos nodos en un análisis bayesiano va a venir determinado por su probabilidad posterior (Pp), siendo el límite de aceptación, dado que se trata de una probabilidad un valor entre 90-95. La gran ventaja de esta medida

es que la Pp se calcula en base a la misma distribución con la que se estima el árbol óptimo, mientras que el Bv requiere reanalizar los datos múltiples veces.

Marcadores moleculares

Los marcadores moleculares han demostrado ser una herramienta muy útil para estudiar diferentes procesos evolutivos (Frankham *et al.,* 2002). La selección de los marcadores más apropiados debe hacerse en base a distintos parámetros, como nivel de polimorfismo, tasa de mutación, modo de herencia (uniparental o biparental) y tipo de expresión (dominante o codominante) (Hillis *et al.*, 1996; Zhang y Hewitt, 2003; Avise, 2004). De este modo, las diferentes clases de marcadores genéticos nos proporcionan niveles de resolución complementarios para estudiar la historia evolutiva de las especies a distintas escalas temporales.

Los resultados obtenidos con diferentes marcadores no siempre han de mostrar el mismo tipo de señal, ya sea porque pueden estar sometidos a efectos diferenciales de deriva o mutación (Buonaccorsi *et al.*, 2001) o porque podemos estar ante genes parálogos que van a hacer que especies con orígenes evolutivos distintos aparezcan emparentadas debido a fenómenos de duplicación de genes (Page y Holmes, 1998).

En los últimos años, el número de marcadores empleados para analizar tanto las relaciones filogenéticas como la estructura poblacional en invertebrados se ha incrementado de manera exponencial. Los genes mitocondriales ARNr 16S y el citocromo oxidasa I (COI) son los más comúnmente empleados para estudiar relaciones a nivel de género y especie (Harrison, 2004; Blanquer y Uriz, 2007; Pérez-Losada *et al.*, 2007), y entre los marcadores nucleares, genes como el ARNr 18S o el ARNr 28S son empleados en estudios filogenéticos por encima del nivel taxonómico de género, siendo los microsatélites más adecuados para estudios de genética de poblaciones debido a su alta variabilidad. El empleo de más de un gen con tasas de evolución diferentes es altamente recomendable, ya que nos permite obtener reconstrucciones más robustas e interpretar, como se ha indicado, las filogenias a distintas escalas temporales.

Marcadores mitocondriales

La mayor parte de trabajos enfocados a resolver las relaciones filogenéticas entre especies, tanto de grupos terrestres como marinos, utilizan genes mitocondriales. El ADN mitocondrial es una molécula de doble hélice, circular y con un tamaño alrededor de 16000 pares de bases. Generalmente está constituida por 37 genes, 22 codificantes de ARNs de transferencia, 2 ARNs ribosomales, 13 ARNs mensajeros y una región no codificante que regula su replicación (Desjardins y Morais, 1990).

El genoma mitocondrial animal presenta una serie de características por las que resulta muy adecuado para estudios poblacionales y filogenéticos a distintos niveles taxonómicos. Se trata de una molécula haploide, no recombinante, con tasas de mutación altas (entre 5-10 veces superior a la de genes nucleares de copia única) y con herencia predominantemente materna, por lo que su tamaño efectivo poblacional es un cuarto del de los *loci* nucleares. Su alta variabilidad, incluso a nivel intraespecífico, lo hace especialmente útil para estudiar fenómenos evolutivos recientes (Avise, 2004), aunque también presenta algunas limitaciones y problemas que son necesarios tener en cuenta a la hora de realizar un estudio filogenético, como son la amplificación de pseudogenes, heteroplasmia o saturación de los marcadores. Es especialmente importante la presencia de pseudogenes, copias de genes mitocondriales que han migrado al núcleo donde acumulan numerosas mutaciones perdiendo su funcionalidad. Su amplificación es bastante común en crustáceos cuando se está trabajando con el gen COI (Williams y Knowlton, 2001; Song *et al.*, 2008; Schubart, 2009); sin embargo, la alta variabilidad de ese gen y su fácil reproducibilidad siguen haciendo que sea uno de los marcadores más comúnmente utilizados.

Los genes mitocondriales ribosomales ARNr 12S y ARNr 16S y el gen codificante COI son los más ampliamente utilizados tanto en estudios poblacionales como en filogenias. Posiblemente la razón fundamental de su uso es la disponibilidad de cebadores universales que minimizan el tiempo de laboratorio, además de permitir efectuar comparaciones con la amplia base de datos nucleotídica de estos tres genes en "GenBank". Los dos genes ribosomales presentan tasas de evolución similares y por tanto suelen proporcionar un mismo tipo de señal filogenética. Por otro lado, la

alta variabilidad entre especies del gen COI lo convierte en uno de los mejores candidatos para analizar las relaciones en niveles taxonómicos bajos.

Aunque este tipo de genes también pueden resultar útiles para resolver las relaciones filogenéticas en los nodos más basales de las filogenias, es necesario testar el efecto de la saturación en cada una de las posiciones (principalmente en las terceras posiciones de los codones) y trabajar con modelos nucleotídicos que incorporen la posibilidad de múltiples mutaciones dentro de un mismo sitio (Palero *et al.,* 2009; Toon *et al.,* 2009).

Marcadores nucleares

El uso de genes nucleares en combinación con genes mitocondriales aporta un nivel de resolución adicional a nuestra filogenia, incrementando las posibilidades de poder reconstruir la verdadera historia del grupo. Los genes nucleares presentan un tamaño efectivo poblacional mayor y en promedio unas tasas de mutación menores que los genes mitocondriales (Moriyama y Powell, 1997), por lo que son más adecuados para resolver las relaciones de los nodos filogenéticos más profundos (Chu *et al.*, 2009).

Recientemente se han incorporado nuevos genes nucleares al estudio de sistemática en decápodos, los cuales parecen ser muy prometedores para resolver relaciones en niveles taxonómicos elevados como familia y superfamilia (Tsang *et al.*, 2008; Ma *et al.*, 2009). Sin embargo, el número de marcadores nucleares disponibles para estudiar las relaciones filogenéticas a nivel de género y especie en decápodos es bastante limitado (Toon *et al.*, 2009). Los genes ribosomales ARNr 18S y ARNr 28S son los más ampliamente utilizados (Ahyong y O'Meally, 2004; Ahyong, 2007). Su tasa de evolución varía entre y dentro de cada uno de estos genes, siendo más conservado el ARNr 18S y por lo tanto mostrando valores de divergencia menores entre especies (Hillis y Dixon, 1991; Toon *et al.*, 2009). El hecho de que sean genes no codificantes para proteínas hace que presenten regiones hipervariables con un gran número de inserciones y deleciones, las cuales son más comunes a medida que aumentamos el nivel taxonómico de estudio. Por tanto, esas regiones requieren una atención especial durante la fase analítica de los datos, ya que un mal alineamiento podría desembocar en una sobreestimación de los valores reales de divergencia.

Biogeografía

En el medio marino, la virtual falta de barreras geográficas ha hecho que históricamente los eventos de especiación alopátrica se consideraran como raros en especies ampliamente distribuidas y con desarrollos larvarios de tipo planctotrófico, asumiéndose que debían tratarse de poblaciones panmícticas con poca estructuración genética (Palumbi, 1992). Bajo ese escenario, lo esperable sería encontrar poblaciones con un flujo génico alto y tasas de especiación bajas; sin embargo, son muchos los casos en los que se han observado procesos de especiación en taxones que supuestamente poseen grandes capacidades de dispersión (Barber *et al.*, 2002; Taylor y Hellberg, 2005; Waters *et al.*, 2005).

En la actualidad, la importancia de la dispersión para explicar tanto procesos de especiación como patrones biogeográficos es cada vez más reconocida, y está considerado como uno de los procesos más determinantes en la generación de diversidad biológica en islas oceánicas y en el medio marino (Cowie y Holland, 2006). La utilización de reconstrucciones filogenéticas para inferir patrones biogeográficos se remonta a los orígenes de la teoría cladista, que proponía que la distribución de los linajes en las distintas ramas podía aportar información sobre su origen geográfico. Desde entonces, las filogenias han sido ampliamente usadas para reconstruir áreas ancestrales, identificar las causas que explican la distribución actual de las especies y detectar eventos biogeográficos (Ree y Sanmartín, 2009).

Las primeras metodologías que se desarrollaron se basaban en el principio de parsimonia y consideraban las dispersiones como sucesos poco probables, siendo fijados *a priori* en el análisis (Humphries y Parenti, 1999). Por tanto, la dispersión era incorporada como un evento *ad hoc* para explicar reconstrucciones biogeográficas que no podían atribuirse sólo a un modelo vicariante (Brooks y McLennan, 2001). Por otro lado, el coste de los eventos no era estimado directamente de los datos, sino que debía ser fijado *a priori*, dando un mayor coste a los eventos de dispersión que a los de vicarianza o extinción, lo que resultaba en una subestimación del número de dispersiones (Sanmartín y Ronquist, 2004).

Recientemente se han desarrollado nuevos métodos biogeográficos como los modelos "Dispersal-Extinction-Cladogenesis" (DEC) y "Bayesian island biogeography" (Ree y Smith, 2008; Sanmartín *et al.*, 2008) que permiten integrar tiempo, vicarianza, dispersión, extinción e incertidumbre filogénetica bajo un mismo modelo, estimando el coste de tales eventos directamente de los datos. Bajo estos nuevos modelos, la topología de un árbol es considerada como una secuencia jerárquica entre ancestros-descendientes, por lo que la longitud de rama va a ser un indicativo de la cantidad de cambio evolutivo en relación al tiempo.

La posibilidad de incorporar el tiempo de evolución en la reconstrucción biogeográfica es una de las principales ventajas que aportan estas nuevas metodologías ya que permiten integrar datos de un gran número de fuentes de información como fósiles, eventos tectónicos, reconstrucciones paleoclimáticas, cambios en el nivel del mar, etc. (Ree y Sanmartín, 2009).

Concretamente el modelo DEC asume que el área geográfica donde una especie está distribuida es un carácter heredable a lo largo del tiempo (Ree *et al.*, 2005; Ree y Smith, 2008). Bajo este procedimiento, la dispersión y la extinción son tratadas como procesos que causan eventos de expansión y contracción de los rangos de distribución. Por defecto, la tasa de dispersión de un área a otra y la tasa de extinción dentro de un área son uniformes en todas las áreas y constantes en todas las ramas de la filogenia (modelo sin restricciones, Figura 2). Sin embargo, estas asunciones son poco probables en sistemas naturales y el modelo puede restringirse de modo que se asuma una mayor probabilidad de dispersión entre áreas adyacentes que entre áreas disyuntas, ya sea como resultado del movimiento de placas tectónicas a lo largo del tiempo, la presencia de barreras, tipo de desarrollo larvario… (modelo restringido, Figura 2).

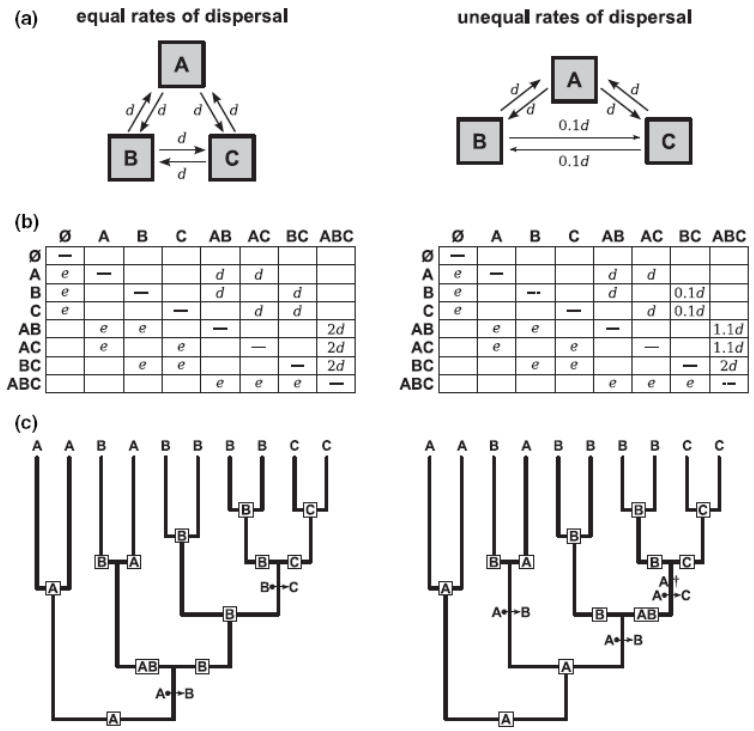


Figura 2. Modelo DEC sin restricciones vs modelo restringido. a) Tasas de dispersión entre áreas, b) Matriz de probabilidad de dispersión entre los distintos rangos geográficos y c) Filogenia resultante de cada modelo con los eventos de extinción y dispersión mapeados sobre cada nodo (tomado de Ree y Sanmartín, 2009).

Este modelo ha sido principalmente empleado para inferir patrones biogeográficos en plantas asociadas al medio continental o a islas oceánicas (Ree y Smith, 2008; Roquet *et al.*, 2009; Smith, 2009), habiendo mostrado estos primeros trabajos un gran potencial para analizar la historia geográfica de taxones cuya distribución es principalmente mediada por eventos dispersivos. De ser así, probablemente no hay escenario más apropiado que el medio marino para aplicar este tipo de metodologías (Trewick y Cowie, 2008), por lo que en el presente trabajo, realizamos una primera evaluación de la utilidad de este método para inferir la historia biogeográfica de un taxón marino.

Familia Galatheidae (Crustacea: Anomura)

Los crustáceos decápodos del infraorden Anomura MacLeay, 1838 han sido objeto de amplias revisiones taxonómicas durante las últimas décadas (Martin y Davis, 2001; McLaughlin *et al.*, 2007), lo que ha derivado en la descripción de un gran número de taxones, incluyendo nuevas familias como Pylojacquesidae (McLaughlin y Lemaitre, 2001), Blepharipodidae (Boyko, 2002) y Kiwaidae (Macpherson *et al.*, 2005). En la actualidad su clasificación abarca 7 superfamilias, 17 familias, 157 géneros y aproximadamente unas 2500 especies (McLaughlin *et al.*, 2007).

Dentro de los crustáceos decápodos, el infraorden Anomura muestra la mayor disparidad de planes corporales, incluyendo desde formas asimétricas como en los cangrejos ermitaños a formas similares a las de los cangrejos verdaderos (braquiuros) como se observa en litótidos o porcelánidos (Ahyong *et al.,* 2009). La gran similitud morfológica de algunas familias de anomuros con cangrejos braquiuros parece estar relacionada con un proceso de carcinización (adquisición de un abdomen ancho y calcificado y reducción del abdomen con plegamiento bajo el tórax), existiendo evidencia morfológica y molecular que muestra que dicho fenómeno ha ocurrido de manera independiente en los distintos linajes de Anomura (McLaughin y Lemaitre, 1997; Morrison *et al.,* 2001). La hipótesis más aceptada plantea que estas formas descienden de formas ermitañas (Cunningham *et al.,* 1992; Richer y Scholtz, 1994); sin embargo, existe controversia al respecto (McLaughin y Lemaitre, 1997) y trabajos recientes sugieren un origen distinto (R. Lemaitre, pers. com.). En términos ecológicos, los anomuros muestran un gran número de adaptaciones, habiendo colonizado desde sistemas dulceacuícolas hasta sistemas de fuentes hidrotermales en profundidades abisales (Zeldis, 1985; Davie, 2002). Esta gran diversidad, tanto en términos ecológicos como morfológicos, convierte el infraorden Anomura en un grupo particularmente interesante para investigar el cambio de forma en crustáceos desde un punto de vista filogenético.

Entre los decápodos Anomura, la superfamilia Galatheoidea incluye las familias Chirostylidae Ortmann, 1892, Galatheidae Samouelle, 1819 y Porcellanidae Haworth, 1825, habiendo sido las familias Aeglidae Dana, 1852 y Kiwaidae Macpherson *et al.,* 2005 recientemente excluidas y asignadas a nuevas superfamilias

(McLaughlin *et al.*, 2007). El origen monofilético de la superfamilia Galatheoidea es muy cuestionado, y trabajos previos basados en caracteres morfológicos reproductivos (Tudge, 1997) y más recientemente en caracteres larvarios (Clark y Ng, 2008) no apoyan la existencia de un origen común. De hecho, la última revisión del grupo, basada en caracteres moleculares y morfológicos, propone la siguiente clasificación: superfamilia Galatheoidea (Galatheidae + Porcellanidae), superfamilia Aegloidea (Aeglidae) y se establece la superfamilia Chirostyloidea para incluir a las familias Chirostylidae y Kiwaidae (Schnabel, 2009). Por tanto, no existe consenso acerca de las relaciones filogenéticas dentro de la superfamilia y futuros trabajos incorporando nuevos caracteres morfológicos, tanto adultos como larvarios, y la inclusión de nuevos marcadores moleculares ayudarán a clarificar la sistemática del grupo.

El término anglosajón "squat-lobster" es empleado comúnmente para referirse a las familias de decápodos anomuros Galatheidae, Chirostylidae y Kiwaidae. Estas tres familias conforman una fauna abundante, diversa y distribuida en todos los hábitats marinos del mundo, por lo que no es de extrañar que recientemente el proyecto COntinental MARGin Ecosystems (COMARGE) del "Census of Marine Life" (CoML) promoviese la celebración de un simposio reuniendo a diez taxónomos de estos grupos (S. Ahyong, K. Baba, A. Bermúdez, P. Cabezas, C.W. Lin, E. Macpherson, M. Nizinski, G. Poore, C. Rodrigues y K. Schnabel) en Nueva Zelanda en Septiembre de 2007. Durante el mismo se evaluó el conocimiento actual del grupo, elaborándose un catálogo mundial con todas las especies descritas hasta la fecha y una base de datos bibliográfica de libre acceso (Baba *et al.*, 2008, http://www. decapoda.nhm.org, ver Anexo I).

La familia Galatheidae (galateidos) es la más diversa de las tres y en el momento de publicación de dicho catálogo incluía un total de 678 especies clasificadas en 34 géneros, habiéndose descrito a lo largo de estos dos últimos años un total de 21 nuevas especies (Tabla 3). A pesar de que la taxonomía de la familia se considera razonablemente estable, nuevos géneros y especies son descritos anualmente, por lo que parece que aún estamos lejos de conocer la diversidad real del grupo. Aproximadamente un 50% de las especies de galateidos han sido descritas en

los últimos veinte años, en parte debido a la revisión de material procedente de campañas históricas como el *Albatross* (Baba, 2005) y, por otro lado, debido al intenso muestreo llevado a cabo por países como Australia y Francia en aguas del Pacífico Suroeste como Nueva Caledonia, Fiji, Tonga, Vanuatu, Queensland… (Macpherson, 1994; Saint-Laurent y Poupin, 1996; Baba, 2005; Ahyong, 2007).

Tabla 3. Número de especies por género de la familia Galatheidae y su distribución en las principales cuencas oceánicas (modificado de Baba *et al.*, 2008).

Género	Atlántico	Índico	Pacífico	Total especies
Agononida	2	2	29	33
Alainius			1	1
Allogalathea		2	4	4
Allomunida			1	1
Anomoeomunida	1			1
Anoplonida			3	3
Babamunida		1	5	6
Bathymunida		1	13	14
Cervimunida			2	2
Coralliogalathea		1	1	1
Crosnierita			4	4
Enriquea			1	1
Fennerogalathea		1	1	2
Galacantha	4	4	7	9
Galathea	15	22	43	70
Heteronida			3	3
Janetogalathea			1	1
Laureia		1	2	2
Leiogalathea	1		1	2
Munida	43	26	186	252
Munidopsis	71	50	132	224
Nanogalathea		1		1
Neonida			1	1
Onconida			5	5
Paramunida		1	26	26
Phylladiorhynchus		4	3	5
Plesionida			3	3
Pleuroncodes			2	2
Raymunida		2	10	11
Sadayoshia		1	2	2
Setanida			1	1
Shinkaia			1	1
Tasmanida			1	1
Torbenella			3	3
Total	137	120	498	698

Caracteres morfológicos

Los caracteres diagnósticos de la familia Galatheidae, compartidos con otros anomuros, son la presencia de cinco pares de patas torácicas (pereiópodos). El primer par está modificado a modo de pinzas (quelípedo), siendo elongado y esbelto. Los siguientes tres pares son más cortos y representan las patas marchadoras. El quinto par está reducido, plegado y generalmente se encuentra escondido bajo el caparazón. El cuerpo es simétrico, con los esternitos torácicos plegados contra el abdomen y los urópodos y el telson formando una ancha cola. Los machos adultos generalmente portan un par de apéndices abdominales denominados pleópodos, estando el primer o los dos primeros pares modificados en estructuras copuladoras (gonópodos). En el caso de las hembras el primer par de pleópodos está siempre ausente (Baba, 2005; Baba *et al.*, 2008). La identificación taxonómica de galateidos se basa principalmente en caracteres morfológicos externos del caparazón, rostro, esternitos torácicos, quelípedos, pereiópodos, maxilípedos y las estructuras de la antena y anténula (Figuras 3 y 4).

La morfología larvaria ha sido utilizada de manera habitual como fuente taxonómica para diferenciar géneros de crustáceos decápodos (Schubart *et al.*, 2002). En galateidos, el conocimiento sobre su desarrollo larvario es muy escaso (Konishi y Saito, 2000; Fujita y Shokita, 2005; Guerao *et al.*, 2006), principalmente debido a la dificultad para obtener hembras ovígeras de aguas profundas. Actualmente, sólo se conoce el desarrollo completo de la especie *Pleuroncodes planipes* Stimpson, 1860 y de otras pocas pertenecientes a géneros distribuidos en aguas someras (p.e. *Galathea* Fabricius, 1793 y *Sadayoshia* Baba, 1969). En todos los casos, el ciclo de desarrollo se caracteriza por tener cuatro o cinco estadios de zoea y una megalopa antes de alcanzar la forma de juvenil (Figura 5).

Por otro lado, aunque el color de los ejemplares parece ser útil para diferenciar especies en determinados géneros como *Raymunida* Macpherson y Machordom, 2000, éste no es un carácter habitualmente empleado puesto que gran parte del material pierde su color original tras su conservación.

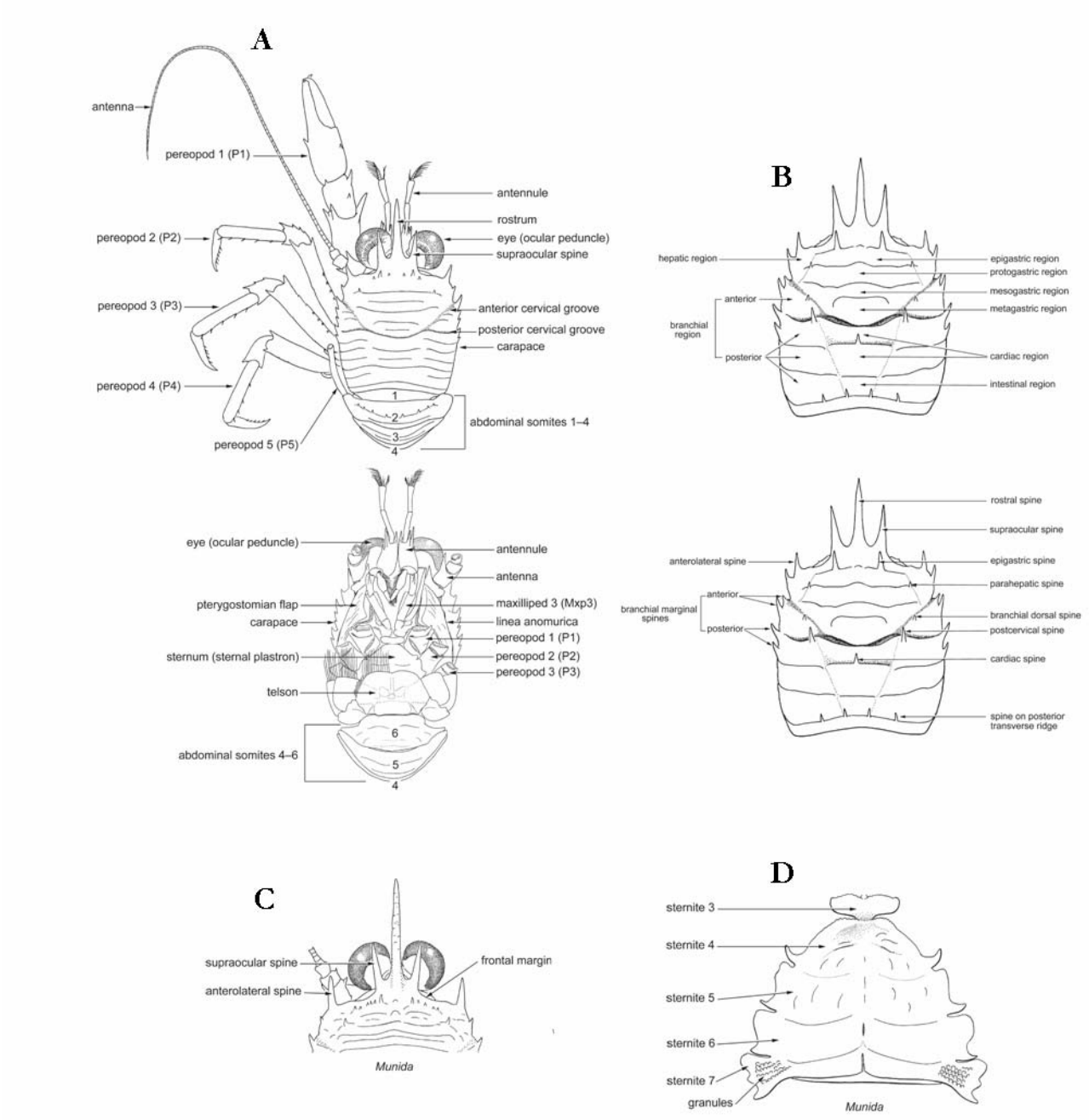


Figura 3. Morfología externa de un galateido. A) Vista dorsal y ventral; B) Regiones y espinas del caparazón; C) Parte anterior del caparazón; D) Esternitos torácicos (tomado de Baba *et al.*, 2009).

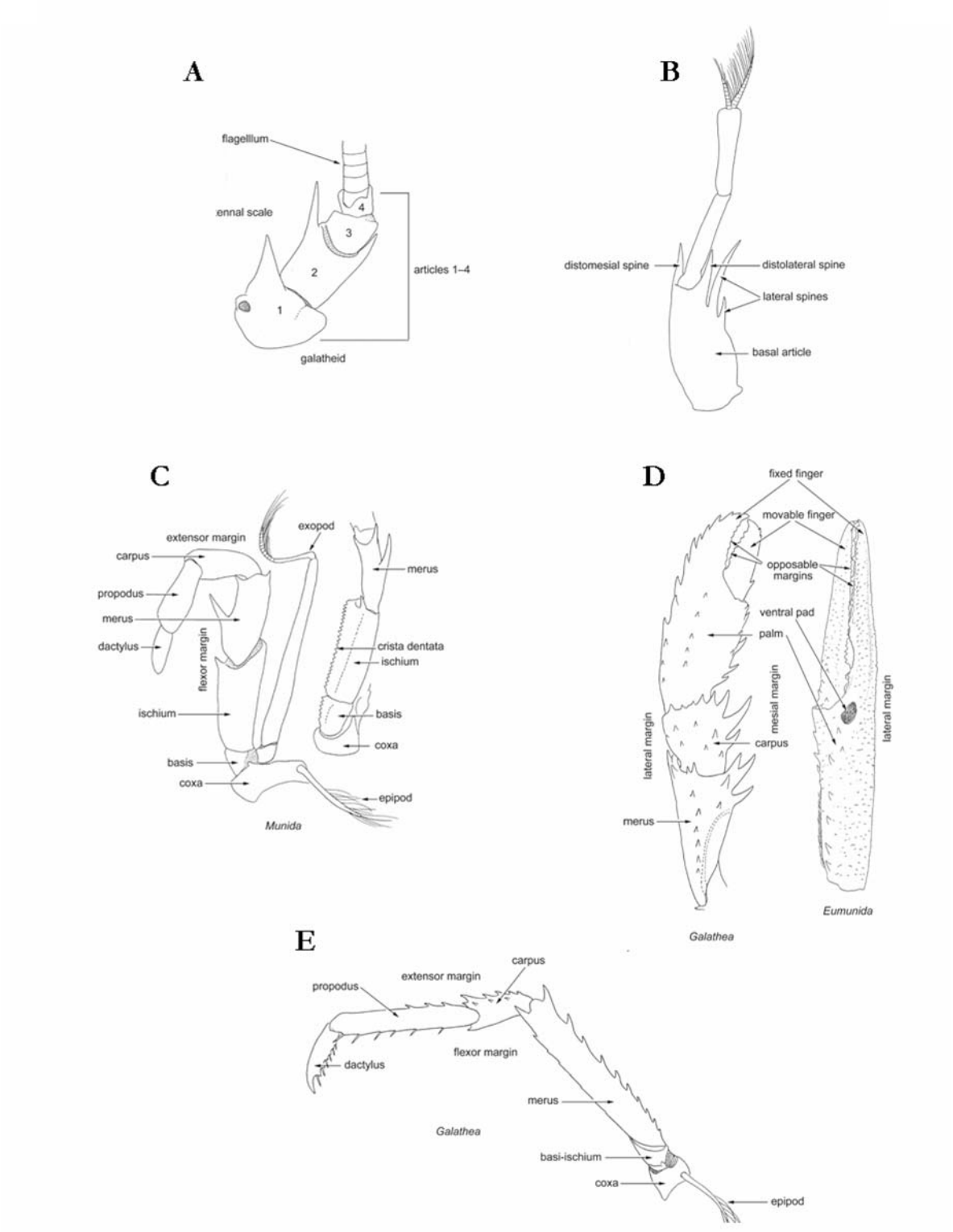


Figura 4. Morfología externa de un galateido. A) Antena; B) Anténula; C) Maxilípedo (Mxp3), vista lateral y ventral; D) Pereiópodo 1 (P1) vista dorsal; E) Pereiópodo 2 (P2) vista lateral (tomado de Baba *et al.*, 2009).

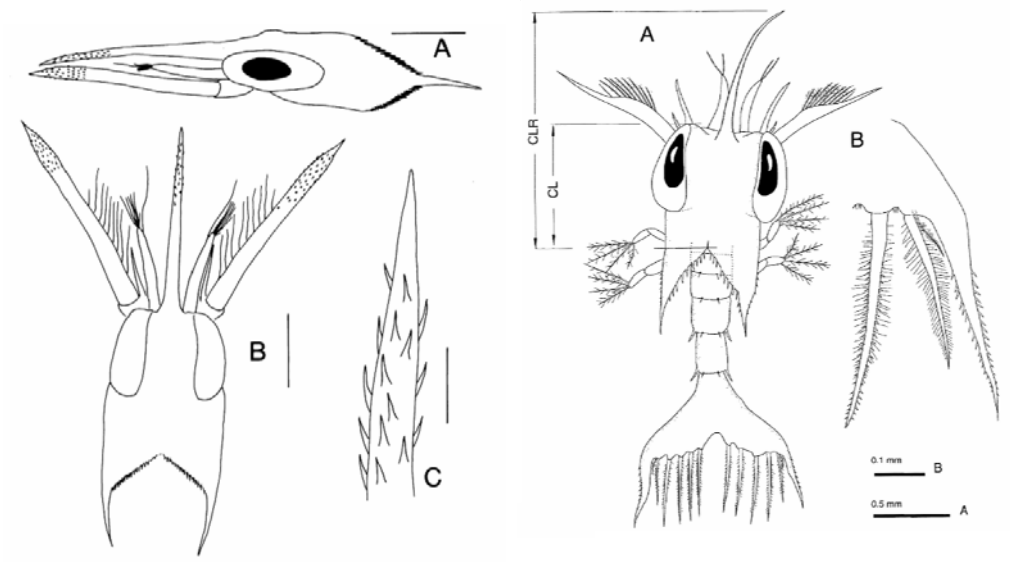


Figura 5. Izquierda. Morfología de la primera zoea de la especie *Babamunida javieri* (Macpherson, 1994) A) Caparazón en vista lateral, B) Caparazón en vista dorsal, C) Extremo de la espina rostral. Escala A-B 0.5 mm y escala C 0.1mm. Derecha. A) Vista dorsal de la primera zoea de *Agononida incerta* (Henderson, 1888) y B) Telson (tomado de Guerao *et al.,* 2006).

Hábitat

Desde un punto de vista ecológico, las especies de la familia Galatheidae se distribuyen en todos los hábitats marinos del mundo, desde aguas superficiales hasta profundidades superiores a los 5.000 metros, tanto en fondos duros como blandos y ocasionalmente asociados a organismos sésiles como corales, crinoideos, gorgonias y esponjas (Figura 6) (Baba, 1988; Zainal, 1990). La mayor parte de especies de la familia Galatheidae presentan hábitos bentónicos, excepto ciertas especies como *Munida gregaria* (Fabricius, 1793) y *Pleuroncodes monodon* (Milne Edwards, 1837) que tienen una fase pelágica durante su ciclo vital, lo cual la convierte en una de las pocas especies de galateidos sometidas a explotación pesquera (Roa y Bahamonde, 1993).

Trabajos previos han mostrado una clara estructuración de la fauna de galateidos en profundidad, de modo que cada franja batimétrica (plataforma, talud, llanura abisal, etc.) está caracterizado por la presencia de unos determinados géneros (Macpherson *et al.*, 2010). Así, los géneros *Galathea*, *Sadayoshia* y *Allogalathea* están típicamente asociados con aguas superficiales y plataforma continental (0-200 m). Las especies del género *Munida* Leach, 1820 y géneros cercanos como *Paramunida* Baba, 1988 o *Agononida* Baba y de Saint Laurent, 1996 se distribuyen principalmente en el

talud continental (200-700 m), siendo el género *Munidopsis* Whiteaves, 1784 el más abundante en las zonas abisales, por debajo de los 900 metros.

Figura 6. *Allogalathea babai* (n.sp.) sobre crinoideo y galateidos asociados a sistemas de fuentes hidrotermales.

Relaciones filogenéticas

Las relaciones filogenéticas dentro de la superfamilia Galatheoidea han sido objeto de un gran número de estudios, pero sólo unos pocos trabajos restringidos a las familias Porcellanidae (Stillman y Reeb, 2001), Aeglidae (Pérez-Losada *et al.*, 2002; Pérez-Losada *et al.*, 2004) e Hippidae (Haye *et al.*, 2002) han intentando resolver las relaciones incorporando tanto caracteres morfológicos como moleculares. La sistemática de la familia Galatheidae continúa a la espera de ser resuelta y hasta la fecha son escasos los trabajos que se han centrado en resolver las relaciones internas de la familia (Machordom y Macpherson, 2004; Schnabel, 2009).

La clasificación actual de la familia Galatheidae se basa principalmente en caracteres morfológicos como el número de pleópodos masculinos, la espinulación y la forma del caparazón (Baba y Camp, 1988). El estudio de los genes mitocondriales ARNr 16S y COI permitió constatar el valor filogenético del número de pleópodos masculinos; sin embargo, otros típicamente empleados como el número de espinas en el margen branquial o la espinulación de los segmentos abdominales no mostraron ser filogenéticamente válidos (Machordom y Macpherson, 2004). Esta primera aproximación molecular confirmó la monofilia de géneros como *Paramunida* y *Raymunida* (Figura 7), mientras que enfatizó la necesidad de más estudios para

clarificar el origen de grupos como *Agononida* y sus relaciones con otros géneros. Por otro lado, la monofilia del género *Munida* sólo era apoyada si se excluía como parte del "ingroup" a la especie *Munida callista* (Macpherson, 1994), habiendo revelado un estudio de la presente Tesis su adscripción a un nuevo género.

Distribución y origen del grupo

El océano Pacífico alberga el mayor número de especies y endemismos de galateidos en el mundo. Aproximadamente el 70% de las especies se distribuye en esas aguas, con un total de 17 géneros endémicos de la región en comparación con *Anomoemunida* Baba, 1993 y *Nanogalathea* Tirmizi y Javed, 1980 que son los únicos restringidos a los océanos Atlántico e Índico respectivamente y los géneros *Pleuroncodes* Stimpson, 1860 y *Janetogalathea* Baba y Wicksten, 1997, cuya presencia se limita a las aguas del Pacífico este (Tabla 3).

El escaso registro fósil existente para el grupo (De Grave *et al.*, 2009) sugiere un origen de la familia Galatheidae en el hemisferio sur a finales del Cretácico, hace aproximadamente unos 70 millones de años (Schweitzer y Feldmann, 2000; Feldmann y Schweitzer, 2006). En la región Indo-Pacífica el progresivo movimiento de las placas tectónicas, junto con la desintegración de Gondwana y en combinación con cambios globales de temperatura y en el régimen de las corrientes oceánicas, generó un gran número de nuevos hábitats. Ello debió de promover una rápida diversificación en la fauna existente, habiéndose propuesto para la familia Galatheidae un modelo de especiación marcado por una radiación explosiva acontecida durante el Mioceno (Machordom y Macpherson, 2004).

Dentro del Pacífico, la región del archipiélago Indo-Malayo (IMPA) parece ser el centro de biodiversidad para un gran número de organismos asociados con aguas superficiales o sistemas arrecifales (Renema *et al.*, 2008), decreciendo el número de especies a medida que aumenta la distancia geográfica respecto a esa región (Paulay, 1997; Bellwood y Hughes, 2001). Sin embargo, algunos taxones muestran patrones de diversidad atípicos, con una mayor riqueza de especies en regiones del Pacífico Suroeste (Malay y Paulay, 2009). Entre ellos se encuentran los galateidos de aguas profundas, que concentran el mayor número de especies en la región de Nueva

Caledonia, con un menor número de especies en la región oeste del Pacífico y muy pocas especies en la región central (Baba *et al.*, 2008; Schnabel *et al.*, 2009).

Para la familia Galatheidae, las regiones de Nueva Caledonia y el mar de Coral, por otro lado Indonesia y Filipinas y en última instancia la Polinesia Francesa, parecen representar centros de diversidad independientes en base a la riqueza y nivel de endemismo de las especies que albergan (Macpherson *et al.*, 2010). Además, un reciente estudio biogeográfico examinando las familias Chirostylidae y Galatheidae de Nueva Zelanda, muestra cómo aproximadamente un 36% de las especies son endémicas de la región, lo que sugiere que podría tratarse de una unidad biogeográfica diferente (Schnabel, 2009). Por tanto, en base a los datos actuales parece ser que la familia Galatheidae muestra un alto grado de regionalización en el océano Pacífico con la posible existencia de diferentes centros de especiación.

Desvelar el origen de la diversidad marina en el Indo-Pacífico se muestra como un importante reto para los biólogos evolutivos debido a la compleja historia geológica del área. En los últimos años, el número de filogenias de especies marinas con distribución Indo-Pacífica ha aumentado de manera exponencial, lo que proporciona una excelente oportunidad para testar nuevos métodos biogeográficos (Barber, 2009). La gran mayoría de trabajos de biogeografía marina centrados en aguas del Indo-Pacífico han intentado desentrañar un origen y causas comunes para explicar los altos niveles de biodiversidad y endemismos marinos de la región, aunque la existencia de una única explicación parece poco probable, siendo más plausible la existencia de distintos procesos actuando a diferentes escalas temporales (Bellwood y Meyer, 2008; Barber, 2009). La mayor parte de esas propuestas se han basado en los patrones de diversidad observados en diferentes grupos taxonómicos; sin embargo, sólo unos pocos han propuesto un marco teórico y estadístico en el que se pudieran testar distintos escenarios o hipótesis (Santini y Winterbottom, 2002; Halas y Winterbottom, 2009).

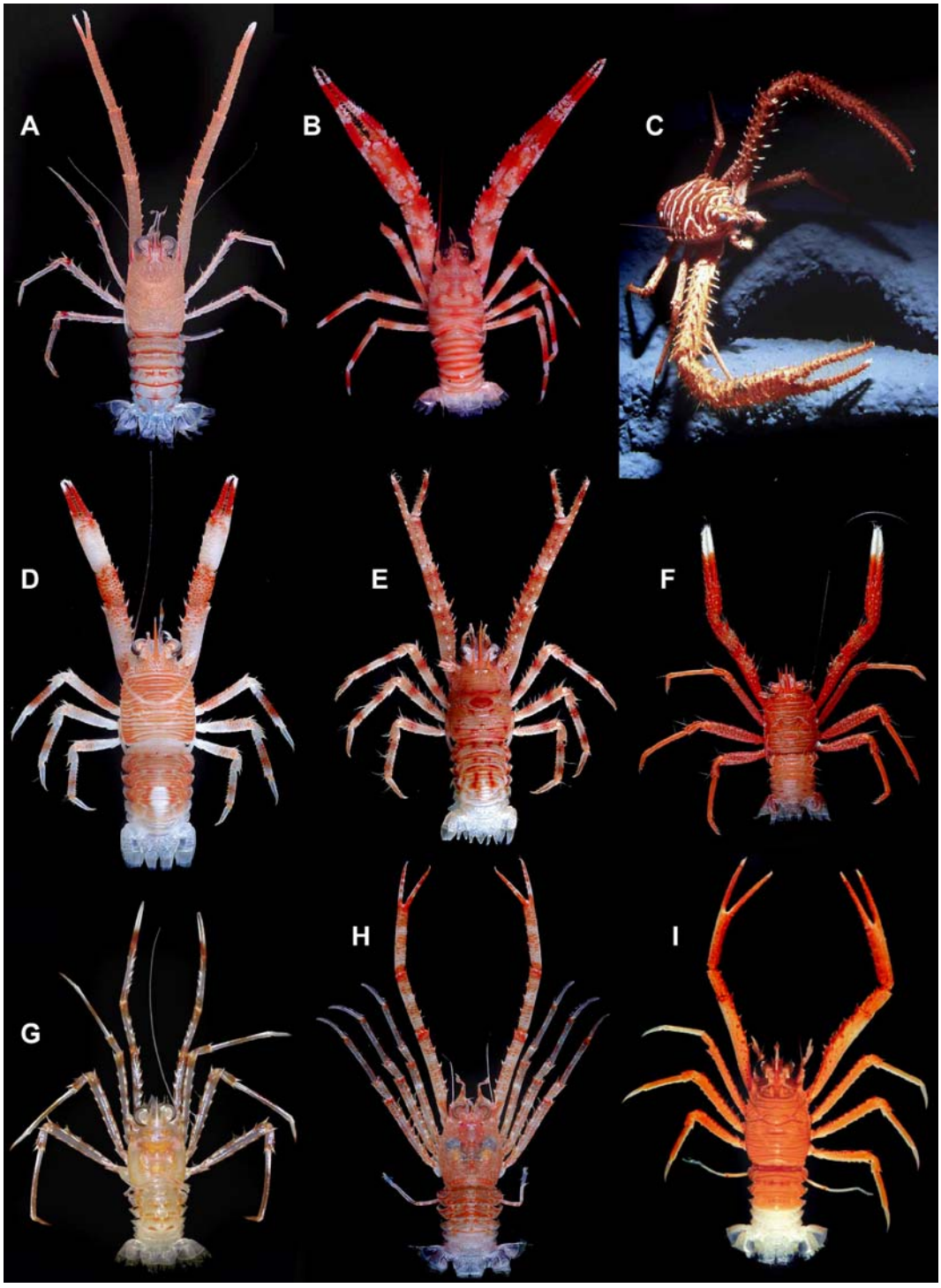


Figura 7. Representación de distintos géneros de la Familia Galatheidae. A, *Enriquea leviantennata* (Baba, 1988). B, *Babamunida* sp. C, *Janetogalathea californiensis* (Benedict, 1902). D, *Munida runcinata* Macpherson, 1994. E, *Munida tyche* Macpherson, 1994. F, *Raymunida erythrina* Macpherson y Machordom, 2001. G, *Agononida marini* (Macpherson, 1994). H, *Paramunida labis* Macpherson, 1996. I, *Cervimunida princeps* Benedict, 1902 (tomado de Baba *et al.,* 2008).

Área de estudio

Como ya se ha indicado, el océano Pacífico alberga una gran biodiversidad marina, la cual ha evolucionado en el contexto de una historia geológica muy compleja. Sólo en sus aguas se distribuyen aproximadamente unas 25.000 islas (más que en todos los demás océanos del mundo juntos). Aunque en la presente Tesis se ha examinado también material procedente del océano Índico y de la región Indo-Pacífica, nuestra principal área de estudio englobó la región central y suroccidental del océano Pacífico (Filipinas, Indonesia, Islas Salomón, Nueva Caledonia, Vanuatu, Fiji, Tonga, Wallis y Futura y la Polinesia Francesa) (Figura 8).

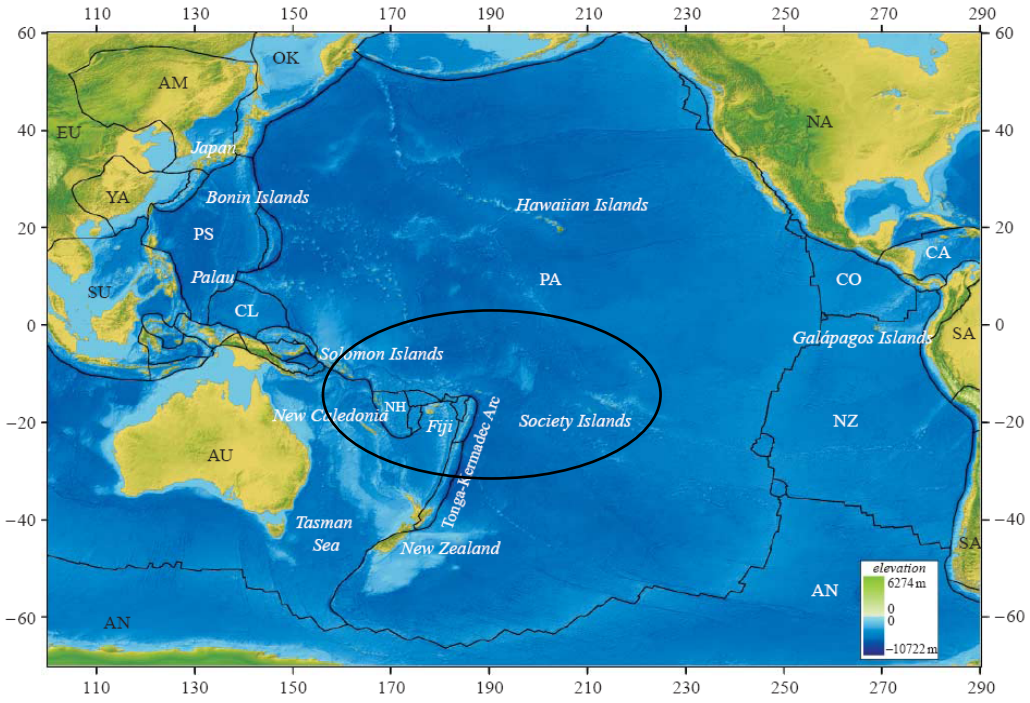


Figura 8. Mapa del océano Pacífico mostrando la localización de las principales islas, placas oceánicas y área de estudio marcada con una elipse. Las abreviaturas de los nombres de las placas corresponden con: AM, Amur; AN, Antártica; AU, Australia; CA, Caribe; CL, Carolina; CO, Cocos; EU, Eurasia; NA, América del Norte; NH, Nuevas Hébrides; NZ, Nazca; OK, Okhotsk; PA, Pacífica; PS, Mar de Filipinas; SA, América del Sur; SU, Sonda; YA, Yangtze (tomado de Neall y Trewick, 2008).

Origen del océano Pacífico

Comprender la evolución de la rica biota que alberga el Pacífico requiere comprender tanto la geología de la cuenca oceánica como la de sus miles de islas. El origen de lo que hoy es el Pacífico se remonta a la escisión del continente Rodinia durante el

Proterozoico. Este continente se escindió en dos creando el antiguo océano Pantalásico y actual océano Pacífico. Aproximadamente 300 millones de años después (Ma), durante el Silúrico, el supercontinente Pangea comenzó a formarse separando los océanos Pantalásico y Paleo-Tetis (Neall y Trewick, 2008). Los primeros signos de ruptura de Pangea acontecieron durante el Mesozoico (aproximadamente hace 180 Ma) y poco después, la expansión del fondo marino hacia el oeste dio lugar a la formación de la presente placa Pacífica (Koppers *et al.*, 2003). El mar de Tetis terminó de formarse durante la era Mesozoica separando los continentes de Gondwana y Laurasia, mientras la placa Índica comenzaba a tomar forma (hace unos 140 Ma) (Figura 9). Finalmente durante el Oligoceno-Mioceno la región alcanzó su forma actual con la colisión de India y Asia, el cierre del mar de Tetis y la colisión de las placas de Australia y Nueva Guinea con el extremo sureste del sistema Filipinas-Halmahera (Hall, 1998). Todos los eventos acontecidos en ese último período produjeron importantes cambios en la geología del Pacífico generando discontinuidades entre las masas de tierra y cambios en las corrientes oceánicas.

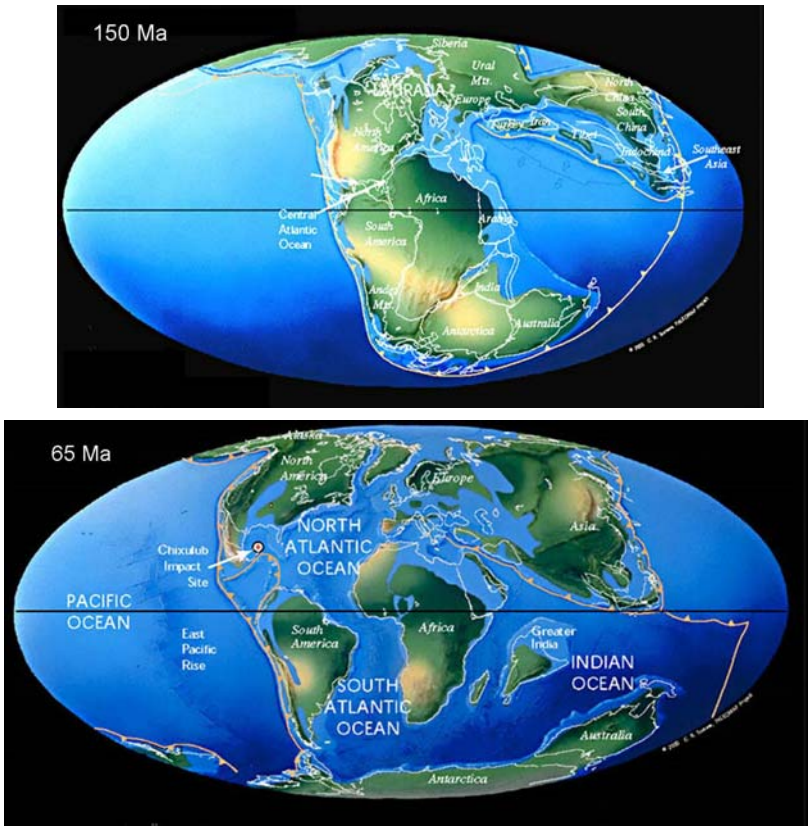


Figura 9. Reconstrucción paleogeográfica durante los períodos Jurásico y Cretácico (tomados de http://www.scotese.com).

Origen de las islas

La gran mayoría de islas del Pacífico son geológicamente jóvenes y de origen volcánico. Algunas de origen continental como Nueva Caledonia se remontan a períodos más antiguos (Cretácico), y otras como las Islas Salomón involucraron sucesivas etapas de formación desde el Eoceno (Neall y Trewick, 2008). El archipiélago de más reciente formación es la Polinesia Francesa, habiéndose datado sus atolones entre 0.3 y 4.8 Ma. A lo largo de la historia geológica del Pacífico cinco grandes procesos han sido responsables de la formación de islas:

1. Formación de cadenas de islas volcánicas por erupciones sucesivas de volcanes sumergidos (p.e. islas Hawaii, Polinesia Francesa).

2. Las islas volcánicas se originan y posteriormente se desplazan con respecto a su lugar de origen. A medida que se desplazan la corteza oceánica se va enfriando y haciéndose más densa con lo que progresivamente se produce un hundimiento. Pueden quedarse a nivel del mar originando islas coralinas llamadas atolones o pueden hundirse a profundidades mayores generando montañas submarinas o guyots (p.e. islas Tuamotu).

3. La flexión de la placa litosférica puede provocar elevaciones de la corteza terrestre en algunas regiones (p.e. algunas regiones del archipiélago de las islas Salomón).

4. Debido tanto a movimientos pasados y presentes de las placas tectónicas, fragmentos de corteza continental se escinden separándose de las grandes masas continentales y originando nuevas islas (p.e. Nueva Caledonia). En la mayor parte de los casos esa ruptura se remonta a períodos incluso anteriores al Eoceno, en contraste con la reciente edad de las islas de origen volcánico.

5. Procesos de subducción en los márgenes de la placa Pacífica (p.e. islas Fiji). A medida que la placa litosférica se hunde por debajo del manto, se generan erupciones de magma que pueden solidificar sin necesidad de emerger o pueden aflorar al exterior y consolidarse como rocas volcánicas.

Origen de la diversidad del Pacífico

Como se ha comentado anteriormente, la diversidad de especies para un gran número de taxones marinos asociados a aguas superficiales (p.e. peces, corales, crustáceos y moluscos) alcanza su máximo en aguas del Pacífico, concretamente en la región del archipiélago Indo-Malayo (Meyer, 2003; Barber y Bellwood, 2005; Briggs, 2007).

Principalmente en base al registro fósil de foramíferos es sabido que durante el Cenozoico la localización de los centros de diversidad marina fue cambiando. De este modo, a comienzos del Eoceno, los mayores picos de biodiversidad marina se concentraban en la región del mar de Tetis, Europa, noroeste de África, Arabia e India (Hoeksema y Renema, 2007). A finales del Eoceno, esa mayor diversidad estaba localizada fundamentalmente en Arabia, y durante el Mioceno el registro fósil de foramíniferos y polen de manglares alcanzaba su máximo de diversidad en la región del sureste del Asia, entre Filipinas y Papua-Nueva Guinea (Figura 10). Se cree que el levantamiento producido durante la colisión de Arabia y Eurasia en la región del mar de Tetis debió generar una gran pérdida de hábitats y merma de las faunas marinas, con la consiguiente relocalización de los centros de diversidad (Renema *et al.*, 2008). Como ya se ha destacado, los complejos procesos geológicos acontecidos en el Indo-Pacífico durante el Oligoceno-Mioceno (Hall, 1998) generaron cambios en el nivel del mar, alteraciones de las corrientes

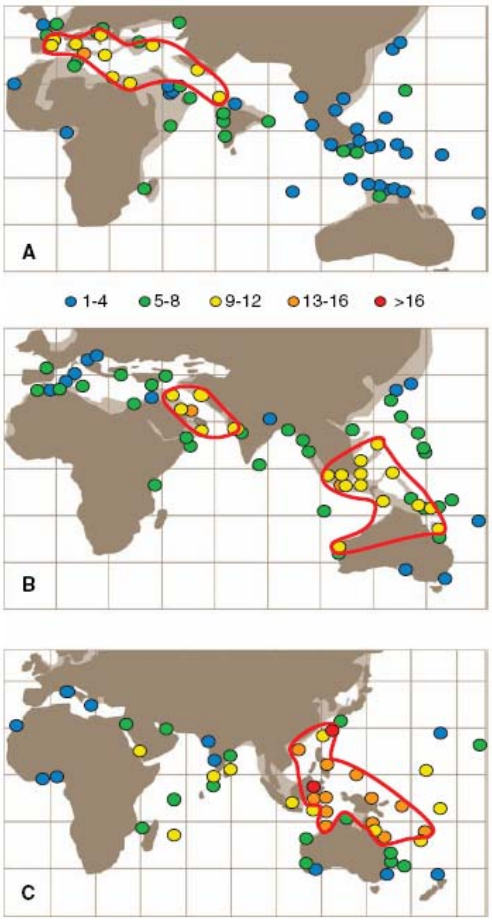
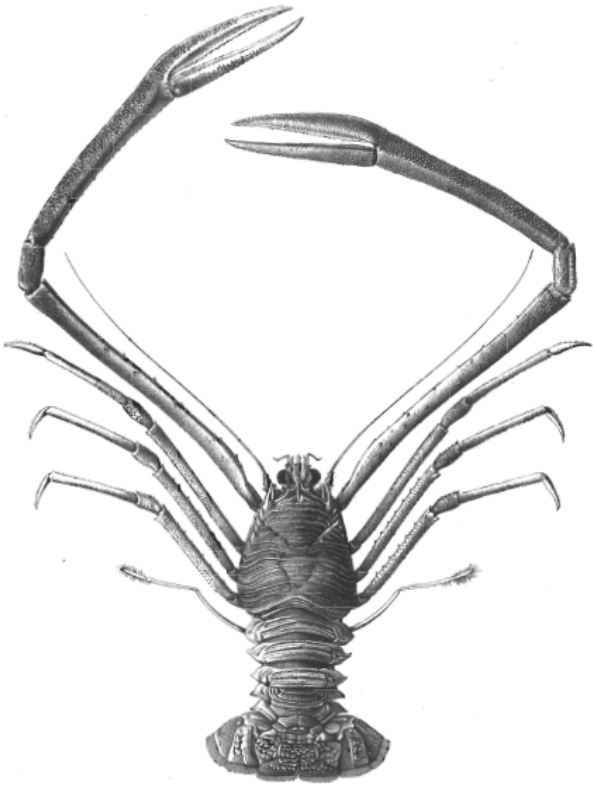


Figura 10. Localización de los centros de alfa diversidad de foraminíferos a lo largo de los últimos 50 Ma. A) Eoceno (42-39 Ma), B) Mioceno (23-26 Ma), C) Actualidad. (tomado de Renema *et al.*, 2008).

oceánicas y cambios en el régimen de temperaturas, que debieron de contribuir significativamente a moldear la distribución y diversificación de la fauna marina (Mora *et al.*, 2003; Barber y Bellwood, 2005; Williams y Duda, 2008). Por tanto, teniendo en cuenta esta información parece claro que la interpretación de los distintos y complejos patrones de diversidad en la región del Pacífico requiere una visión holística, que incluya tanto factores históricos (eventos geológicos) como procesos bióticos y abióticos más recientes, tales como tasas especiación/extinción, dispersión y retención larvaria, disponibilidad de hábitat, patrones de corrientes actuales o producción primaria.



Munida refulgens Faxon, 1893

Objetivos

En la presente Tesis Doctoral se realiza una revisión de la sistemática de distintos géneros de la familia Galatheidae, evaluando la utilidad tanto de caracteres morfológicos como la de distintos marcadores moleculares (mitocondriales y nucleares). De este modo y en combinación con otros análisis, se pretende establecer un marco taxonómico, filogenético y biogeográfico robusto para interpretar la historia evolutiva de la familia. Los objetivos específicos del trabajo son los siguientes:

1. Determinar el grado de variabilidad morfológica a nivel intergenérico e interespecífico para evaluar el valor taxonómico de los caracteres morfológicos.

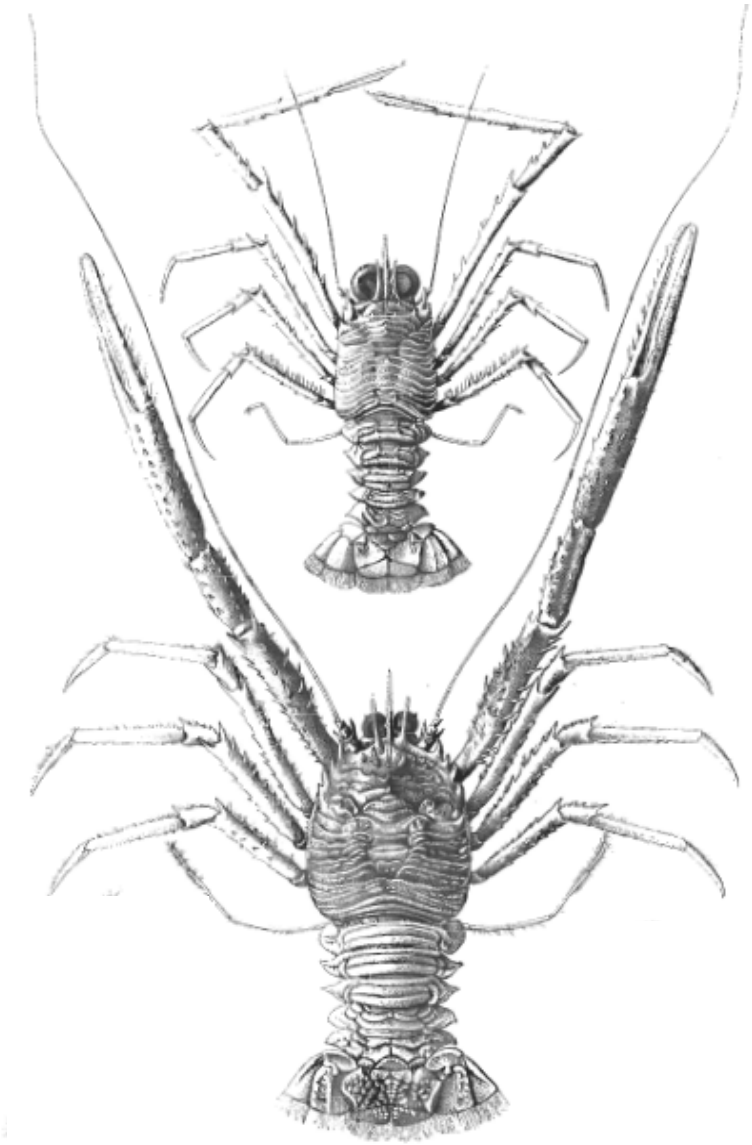
2. Describir e ilustrar los nuevos taxones descubiertos (género y especies).

3. Evaluar y confirmar el valor taxonómico de los caracteres estudiados mediante técnicas moleculares. Reconstruir las relaciones filogenéticas en los géneros *Allogalathea* y *Babamunida*, así como de diversas especies de los géneros *Paramunida* y *Munida,* entre otros. Resolver la posición filogenética de los nuevos linajes y comparar el nivel de resolución de genes mitocondriales y nucleares.

4. Establecer una escala temporal evolutiva para el origen y diversificación de la familia Galatheidae, tomando como modelo el género *Paramunida.*

5. Analizar la historia biogeográfica del género *Paramunida* empleando un método de reconstrucción de áreas ancestrales.

6. Finalmente se pretende integrar las conclusiones obtenidas a través de las distintas aproximaciones con el propósito de mejorar el conocimiento acerca de la biodiversidad e historia evolutiva de la familia Galatheidae.



Munida obesa Faxon, 1893
Munida graciliptes Faxon, 1893

CAPÍTULO I

JOURNAL OF CRUSTACEAN BIOLOGY, 28(1): 68–75, 2008

A NEW GENUS OF SQUAT LOBSTER (DECAPODA: ANOMURA: GALATHEIDAE) FROM THE SOUTH WEST PACIFIC AND INDIAN OCEAN INFERRED FROM MORPHOLOGICAL AND MOLECULAR EVIDENCE

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A B S T R A C T

In a previous phylogenetic analysis of numerous species of the genus *Munida* and related genera from the West Pacific based on molecular and morphological data, the monophyly of this group with the exception of *M. callista* was established. Morphologically, *M. callista* is closely related to *M. brucei*, *M. javieri*, *M. hystrix* and *M. plexaura* showing morphological differences in the shape of the rostrum, the supraocular spines, and the ridges on the epistome with respect to the genus *Munida*. Moreover, the analysis of the mitochondrial genes 16S rRNA and COI showed an independent and monophyletic lineage from the genus *Munida*. Therefore a new genus, *Babamunida*, is proposed to accommodate these five species, based on morphological characters and molecular data.

KEY WORDS: Anomura, DNA, molecular systematics, morphology, taxonomy

INTRODUCTION

Galatheidae Samouelle, 1819 is among the most diverse families of anomuran decapods and now comprises about 30 genera (Baba, 2005). Of these genera, *Munida* Leach, 1820 is perhaps the most varied and is currently represented by more than 200 species (Baba, 1988, 2005; Macpherson, 1994, 2006). In recent years and after the description of more than 100 new species of *Munida* and related taxa from the Pacific and Indian Oceans (Baba, 1988, 2005; Macpherson, 1994, 2006 and references cited therein), the genus was split into different genera, e.g., *Agononida* Baba and de Saint Laurent, 1996, *Crosnierita* Macpherson, 1998, *Enriquea* Baba, 2005, *Munida* Leach, 1820, *Paramunida* Baba, 1988, and *Raymunida* Macpherson and Machordom, 2000.

The phylogenetic analysis of these taxa using molecular and morphological data supported the taxonomic separation into several genera (Machordom and Macpherson, 2004) and pointed to the monophyly of the species of the genus *Munida* from the western Pacific, with the exception of *M. callista* Macpherson, 1994. This species showed the greatest divergence in the two genes sequenced (COI and 16S rRNA) with respect to the other species of the genus *Munida* from this area.

Munida callista is characterized by the presence of three branchial spines along the lateral margin of the carapace; the anterolateral spines are well developed, the pleomeres are unarmed and the lateral parts of the fifth to seventh thoracic sternites lack granules or carinae. Morphologically, *M. callista* is closely related to *M. hystrix* Macpherson and de Saint Laurent, 1991 from French Polynesia, *M. javieri* Macpherson, 1994 from New Caledonia and the Chesterfield, Matthew and Hunter Islands, *M. plexaura* Macpherson and de Saint Laurent, 1991 from New Caledonia and the Chesterfield Islands and *M. brucei* Baba, 1974 from Kenya and Mauritius.

In the present study, we propose a new genus to group together *M. callista*, *M. hystrix*, *M. plexaura*, *M. javieri* and *M. brucei* based on: 1) molecular data from the 16S rRNA and COI for the closely related species (*M. javieri*, *M. hystrix* and *M. plexaura*), and 2) morphological characters that separate the species of the genus *Munida* (type species *M. rugosa* (Fabricius, 1775) from NE Atlantic Ocean) from *M. callista* and related species. The molecular phylogenetic position of *M. hystrix*, *M. javieri*, and *M. plexaura* confirmed their close relationship with *M. callista* and revealed their vast divergence with respect to the other species of the genus *Munida*. In the case of *M. brucei* only the morphological characters were analyzed, due to the lack of material for the molecular analysis. To accommodate these five species, we herein describe a new genus, *Babamunida*.

MATERIALS AND METHODS

Material Analysed

Specimens of species deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN) were used for morphological and molecular analyses. Descriptive data for the first larval stage of *M. javieri* were obtained from Guerao et al. (2006), and compared with those observed here for the first zoea stage of *M. striola* Macpherson and Baba, 1993, *M. gregaria* (Fabricius, 1793) and *M. tenuimana* G.O. Sars, 1872. We sequenced part of the 16S rRNA gene for *M. hystrix*, *M. javieri* and *M. plexaura*, and obtained COI sequence data only for *M. hystrix*. For *M. callista*, we used previous molecular data obtained for this species and others by Machordom and Macpherson (2004).

DNA Extraction and Amplification

Tissue samples were preserved in ethanol and total DNA was isolated by standard proteinase K and phenol/chloroform extraction procedures (Sambrook et al., 1989). The partial 16S rRNA was amplified by polymerase chain reaction (PCR) using the primers 1471 (5′-CCTGTTTANCAAAAACAT-3′) and 1472 (5′-AGATAGAAACCAACCTGG-3′) (Crandall and Fitzpatrick, 1996). The partial COI only was amplified for two specimens of *M. hystrix*, with the following pairs of primers:

LCO1490 (Folmer et al., 1994) and the newly designed COIR1 (5′-ACNTTATATTTTATYTTYGG-3′) and COI-f (5′-GAGCTCCAGATA TAGCATTCC-3′) and COI-r (5′-AGTATAAGCGTCTGGGTAGTC-3′) (van Syoc, 1995).

In a final volume of 50 µl, the PCR mix contained 2 µl of DNA template, 0.16 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer (containing 2 mM $MgCl_2$), 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. The amplification process for the partial 16S rRNA sequence was conducted as follows: 94°C (4 min), 40 cycles at 94°C (45 s), 45.5°C (1 min), 72°C (1 min), and a final extension at 72°C (10 min). Amplification of the COI gene was performed under the same conditions except for a higher annealing temperature (50°C).

The amplified fragments, 549 bp for the 16S rRNA (after within-matrix realignment with other galatheids, Machordom and Macpherson, 2004) and 657 bp for the COI were purified by ethanol precipitation prior to sequencing both strands using "Big Dye Terminator" (Applied Biosystems, ABI) sequencing reactions. Sequences were run on an ABI 3730 Genetic Analyzer (Applied Biosystems). Forward and reverse DNA sequence strands were compared using the Sequencher program (Gene Code) after removing the primer regions. New sequences were deposited in GenBank under accession numbers EF136566-EF136571.

Only the 16S rRNA gene portion was sequenced for all the species of the proposed new genus, thus phylogenetics analyses were performed for this gene only. Parsimony tests were performed using WinClada (Nixon, 2002). Characters were coded as nonadditive, and "island hopping" conducted through 100,000 iterations, with one tree held from each, amb-poly was 10% of the characters sampled, and the random constraint was 10. The evolutionary molecular model that best fitted our data was selected using MODELTEST 3.06 (Posada and Crandall, 1998) under the Akaike information criterion (Akaike, 1974). Sequence analyses were based on the principles of maximum likelihood (ML) and neighbour-joining (NJ) with the model and parameters selected by MODELTEST using the PHYML (Guindon and Gascuel, 2003) and PAUP 4.0b10 package (Swofford, 2002) respectively.

We estimated support in the NJ (2000 pseudoreplications) and ML analyses by bootstrapping (500 pseudoreplications) (Felsenstein, 1985). We also used Bayesian analyses to calculate the posterior probabilities of the nodes in the phylogenetic trees. Four chains were run for 5,000,000 generations and trees prior to log likelihood stabilization were discarded as burn- in.

SYSTEMATICS

Galatheidae Samouelle, 1819
Babamunida n. gen.

Type Species.—*Munida callista* Macpherson, 1994, by present designation.

Included Species.—*B. callista* (Macpherson, 1994), *B. hystrix* (Macpherson and de Saint Laurent, 1991), *B. javieri* (Macpherson, 1994), *B. plexaura* (Macpherson and de Saint Laurent, 1991) and *B. brucei* (Baba, 1974).

Description.—Carapace with transverse ridges, usually granulated. Rostral spine spiniform, carinate dorsally, clearly overreaching supraocular spines; supraocular spines spiniform, carinate dorsally, well developed and not overreaching end of corneae; deep longitudinal grooves between rostrum and supraocular spines; rostral and supraocular anterior carinae, reaching the epigastric region (Figs. 1A, C). Dorsal carapace surface with at least a row of epigastric spines, largest pair usually situated directly behind supraocular spines. Frontal margins oblique, slightly concave. Anterolateral spines present. Branchial margins with 3-4 spines. Second to fourth pleomeres unarmed. Telsonal subdivision incomplete. Fourth thoracic sternite with anterior margin wide, moderately concave; median part or whole posterior margin of third sternite contiguous with fourth sternite; sixth and seventh sternites without granules or keels. Orbit visible in dorsal view, ventral margin of orbit with well developed mesial spine accompanied by additional spine at base. Eyes large, corneae strongly dilated, maximum corneal width equal to or more than 1/3 distance between anterolateral spines. Antennular basal segment with 2 distal spines; 2 additional spines on lateral margin, subdistal spine longer than proximal spine. Antennal basal segment with short distomesial spine short, never exceeding second segment; second segment with well-developed distal spines. Antennal flagellum longer than chelipeds. Epistome with ridge between marginal ridge (mouth) and ventral margin of orbit clearly separated from base of antennal peduncle, without protuberance near marginal ridge; ridge situated at base of antennule scarcely discernible (Figs. 1B, D). Merus of third maxilliped shorter than ischium, rectangular in lateral view, with 2-3 marginal spines along flexor border. Chelipeds moderately slender, elongated, usually longer and stouter in males than in females; palm compressed, as long or shorter than fingers, with row of spines along mesial, lateral and dorsal sides: movable and fixed fingers with row of spines along mesial and lateral margins, respectively. Walking legs long and slender; dactyli slender, slightly curving; flexor margin with spine-like setae. Flexor face of fifth pereiopods lacking brush of plumose setae. Male gonopods present on first and second abdominal segments. Epipods absent from pereiopods.

Etymology.—Besides making reference to *Munida*, the generic name *Babamunida* acknowledges the significant contributions of Keiji Baba to the study of the Galatheoidea. Gender: feminine.

Molecular Phylogeny

The partial COI sequence dataset obtained for *B. callista* and *B. hystrix* consisted of 657 characters, of which 337 were constant, 47 were parsimony uninformative and 273 were parsimony informative. For the 16S rRNA gene sequence analysis, the four species belonging to the new genus were evaluated together with related genera of Galatheidae (*Onconida*, *Plesionida*, *Agononida*, *Heteronida*, *Pleuroncodes*, *Cervimunida*, *Bathymunida*, *Crosnierita*, *Enriquea*, *Leiogalathea*, *Paramunida*, *Munida*, *Raymunida*, and *Alainius*). *Eumunida sternomaculata* de Saint Laurent and Macpherson, 1990 (Chirostylidae) was used as out-group. This gene showed two high variability regions between positions 232 and 292, and 364 and 376. After alignment, the resulting dataset comprised 549 characters, of which 257 were constant, 36 were variable and parsimony uninformative and 256 were parsimony informative.

Divergences among the species of *Babamunida* were in the range 5.2-11.09% for the 16S rRNA and 15.37-15.52% for the COI sequences, lower than almost all intergeneric values (Table 1). Divergence between these four species and other *Munida* species ranged from 11.02 to 16.94% for the16S rRNA gene sequence and 17.04 to 22.52% for COI. The 16S rRNA divergence between species of *Babamunida* and the type species *Munida rugosa* was 11.04 to 14.16%.

The model that best fitted our 16S rRNA gene dataset was the Tamura- Nei + I + Γ model (Tamura and Nei, 1993), which rendered a parameter α of 0.633 and I-value of 0.4106. Molecular phylogenetic analyses based on 16S rRNA indicated that *B. callista*, *B. hystrix*, *B. javieri* and *B. plexaura* constitute a monophyletic assemblage, with high support (Fig. 2). Relationships within the new genus

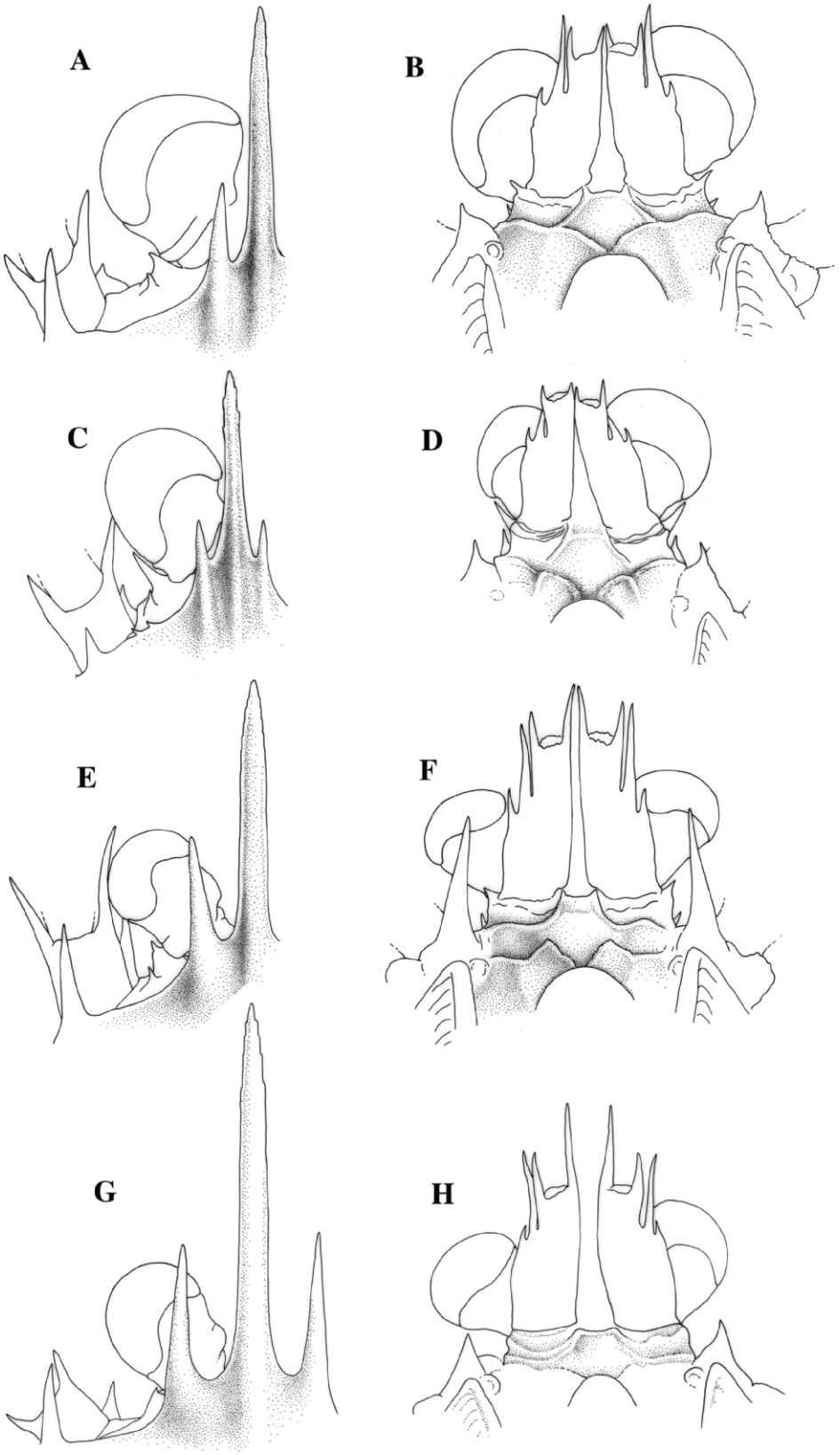


Fig. 1. A, C, E, G, Rostrum, supraocular spines and left orbital region. B, D, F, H, Ventral view of antennules and epistome. A-B, *Babamunida callista*, M, 15.8 mm CL, New Caledonia, cruise Norfolk 2, stn 2048. C-D, *B. hystrix*, M, 12.9 mm CL, French Polynesia, cruise Benthaus, stn 2008. E-F, *Munida rubridigitalis*, ov. F, 14.8 mm, New Caledonia, cruise Biocal, stn 52. G-H, *M. rugosa*. Scale: A, B, D, G, H = 5 mm; C, E, F, I = 2 mm.

Table 1. Molecular divergence ranges (in percentage) for 16S rRNA and COI sequences between *Babamunida* and closed related genera within Galatheidae.

	Range	
	16S rRNA	COI
Agononida	11.33-15.08	16.13-20.39
Alainius	14.99-17.44	16.43-19.78
Bathymunida	13.11-16.41	19.01-20.16
Crosnierita	11.28-15.66	18.41-19.02
Enriquea	15.01-17.01	19.33-21.91
Munida	11.02-16.94	17.04-22.52
Onconida	12.21-15.53	17.65-20.09
Paramunida	13.37-16.76	17.50-20.85
Raymunida	14.70-16.21	18.11-20.71
Plesionida	12.59-15.12	18.29-18.70
Leiogalathea	17.64-19.07	21.30-24.35
Heteronida	13.28-17.46	—
Pleuroncodes	16.71-17.53	19.17-19.93
Cervimunida	13.19-15.55	19.17-20.70

revealed *B. callista* and *B. plexaura* as a sister group, although only indicated by one analysis and with low support, and a second cluster formed by *B. hystrix* and *B. javieri* that was highly supported. The sister group of the new genus was found to be *Crosnierita* (*C. urizae* and *C. yante*, excluding *C. dicata*), always with strong support. Nevertheless, relationships between this group (*Babamunida* + *Crosnierita*) and the remaining groups were unresolved. The Bayesian analysis indicated that the type species, *Munida rugosa*, appears in a basal position with respect to the rest of the species of *Munida*, but also included *Pleuroncodes*, *Cervimunida*, *Raymunida*, *Alainius* and *Enriquea*. *Babamunida* was not a member of this cluster, despite the fact that its members had previously been assigned to the genus *Munida*.

Discussion

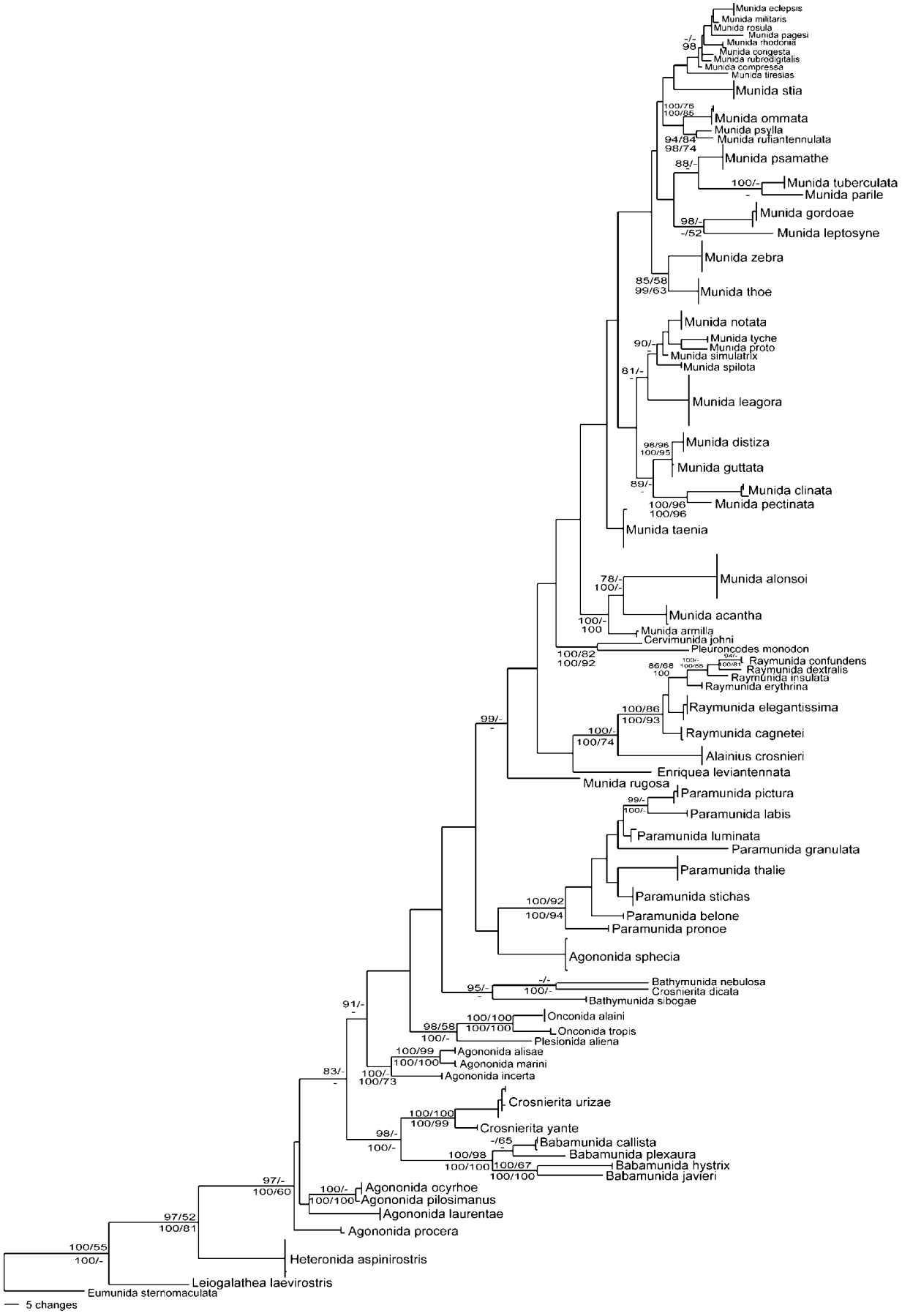
The new genus described here includes *B. callista*, *B. hystrix*, *B. javieri*, *B. plexaura*, and *B. brucei*. The latter species from Kenya and Mauritius is morphologically similar to *B. hystrix* from French Polynesia (Baba, 1974, 2005). However, we have not analysed the different genes of this species and further study will be needed to confirm its taxonomic status. The new genus is morphologically linked to *Munida*. The type species of *Munida* is *M. rugosa*, from the northeastern Atlantic. When we compared specimens of this species (NE Atlantic, MNHN) with most of the SW Pacific specimens included in Macpherson (1994), Machordom and Macpherson (2004) and other papers (see Baba, 2005; Macpherson, 2006), the most conspicuous morphological differences were: 1) the shape of the rostrum and supraocular spines, and 2) the ridges on the epistome. All other characters showed some degree of variability among species and are ineffective for distinguishing between the two genera.

In *M. rugosa* and other species of the genus *Munida*, the rostrum and supraocular spines are dorsally smooth and not carinate (Figs. 1E, G), yet they are carinate in *Babamunida*. Moreover, these carinae reach the anterior portion of the epigastric region (Figs. 1A, C). Also, the grooves between the rostrum and supraocular spines are always deeper in *Babamunida* than in *Munida*.

The ridges on the epistome differ between the two genera. The epistome is the broad median plate extending from the orbit to the mouth, and laterally to the carapace margins at the level of the mouth (see Martin and Abele, 1988 for the terminology). In Galatheidae, this structure has not been used for taxonomic purposes, although some of its characters have been used to distinguish other decapod taxa, e.g., Varunidae (Ng et al., 1999), Cambaridae (Cooper, 2006), Glypheoidea (Schram and Ahyong, 2002). On this plate, a marginal ridge is observed around the mouth. From the anterolateral portion of this marginal ridge, a lateral ridge extends anterolaterally to the carapace. The direction of this lateral ridge clearly differs in the species of *Munida* and *Babamunida*. In *Munida rugosa* and all the other species of *Munida* examined, the lateral ridge ends at the base of the basal antennal segment, at the level of the antennal gland aperture (Figs. 1F, H). In other galatheid genera (*Raymunida*, *Agononida* and *Paramunida*), this ridge runs in a similar direction (Fig. 3). However, in *Babamunida*, the lateral ridge ends at the ventral margin of the orbit, between the antennular and antennal peduncles (Figs. 1B, D, see also Macpherson and de Saint Laurent, 1991). Furthermore, in most species of *Munida* from the SW Pacific (also observed in *Cervimunida princeps* Benedict, 1902), the lateral ridge has a protuberance near the mouth (Fig. 1F). This protuberance is absent in *M. rugosa* (Fig. 1H) and in all species of *Babamunida* (Fig. 1B, D).

The morphology of the zoea I stages has been used as a source of characters to differentiate decapod crustacean genera (Schubart et al., 2002). The zoea I stage of *B. javieri* (Guerao et al., 2006) displays characters not previously described for larvae of *Munida*: namely the presence of a robust posterolateral process on the third pleomere and the $1 + 1 + 4$ pattern of setae on the endopod of the maxillule. The descriptions of the zoea I stages in other *Munida*, such as *M. subrugosa*, *M. tenuimana*, and *M. striola* do not show the process on the third abdominal somite, and the number of setae is $1 + 4$ instead of $1 + 1 + 4$ (see Guerao et al., 2006 for a complete description). This number of setae on the endopod of the maxillule has only been observed in *Cervimunida johni* (Porter, 1903) and *Sadayoshia edwarsii* (Miers, 1884) (see Fagetti, 1960; Fujita and Shokita, 2005). These larval differences would support the separation between *Munida* and *Babamunida*. However, additional data would be necessary to obtain a more complete knowledge of the relationships between larval stages and adult squat lobster genera.

The morphological characters of *Munida brucei* suggest its inclusion in the new genus, although we could not confirm this at the molecular level because of a lack of appropriate material. Our molecular results clearly suggest that *Babamunida* constitutes a well supported monophyletic genus, clearly differentiated from *Munida*. The range of inter-genus distances found between *Babamunida* and *Munida* was higher than the range between *Babamunida* and other related genera (Table 1). The closest related genus of *Babamunida* is *Crosnierita* (*C. urizae* and *C. yante*, but not *C. dicata*). Machordom and Macpherson (2004) suggested this relationship previously, although without statistical support.


Munida eclepsis
Munida militaris
Munida rosula
Munida pagesi
Munida rhodonia
Munida congesta
Munida rubrodigitalis
Munida compressa
Munida tiresias
Munida stia
Munida ommata
Munida psylla
Munida rufiantennulata
Munida psamathe
Munida tuberculata
Munida parile
Munida gordoae
Munida leptosyne
Munida zebra
Munida thoe
Munida notata
Munida tyche
Munida proto
Munida simulatrix
Munida spilota
Munida leagora
Munida distiza
Munida guttata
Munida clinata
Munida pectinata
Munida taenia
Munida alonsoi
Munida acantha
Munida armilla
Cervimunida johni
Pleuroncodes monodon
Raymunida confundens
Raymunida dextralis
Raymunida insulata
Raymunida erythrina
Raymunida elegantissima
Raymunida cagnetei
Alainius crosnieri
Enriquea leviantennata
Munida rugosa
Paramunida pictura
Paramunida labis
Paramunida luminata
Paramunida granulata
Paramunida thalie
Paramunida stichas
Paramunida belone
Paramunida pronoe
Agononida sphecia
Bathymunida nebulosa
Crosnierita dicata
Bathymunida sibogae
Onconida alaini
Onconida tropis
Plesionida aliena
Agononida alisae
Agononida marini
Agononida incerta
Crosnierita urizae
Crosnierita yante
Babamunida callista
Babamunida plexaura
Babamunida hystrix
Babamunida javieri
Agononida ocyrhoe
Agononida pilosimanus
Agononida laurentae
Agononida procera
Heteronida aspinirostris
Leiogalathea laevirostris
Eumunida sternomaculata
5 changes

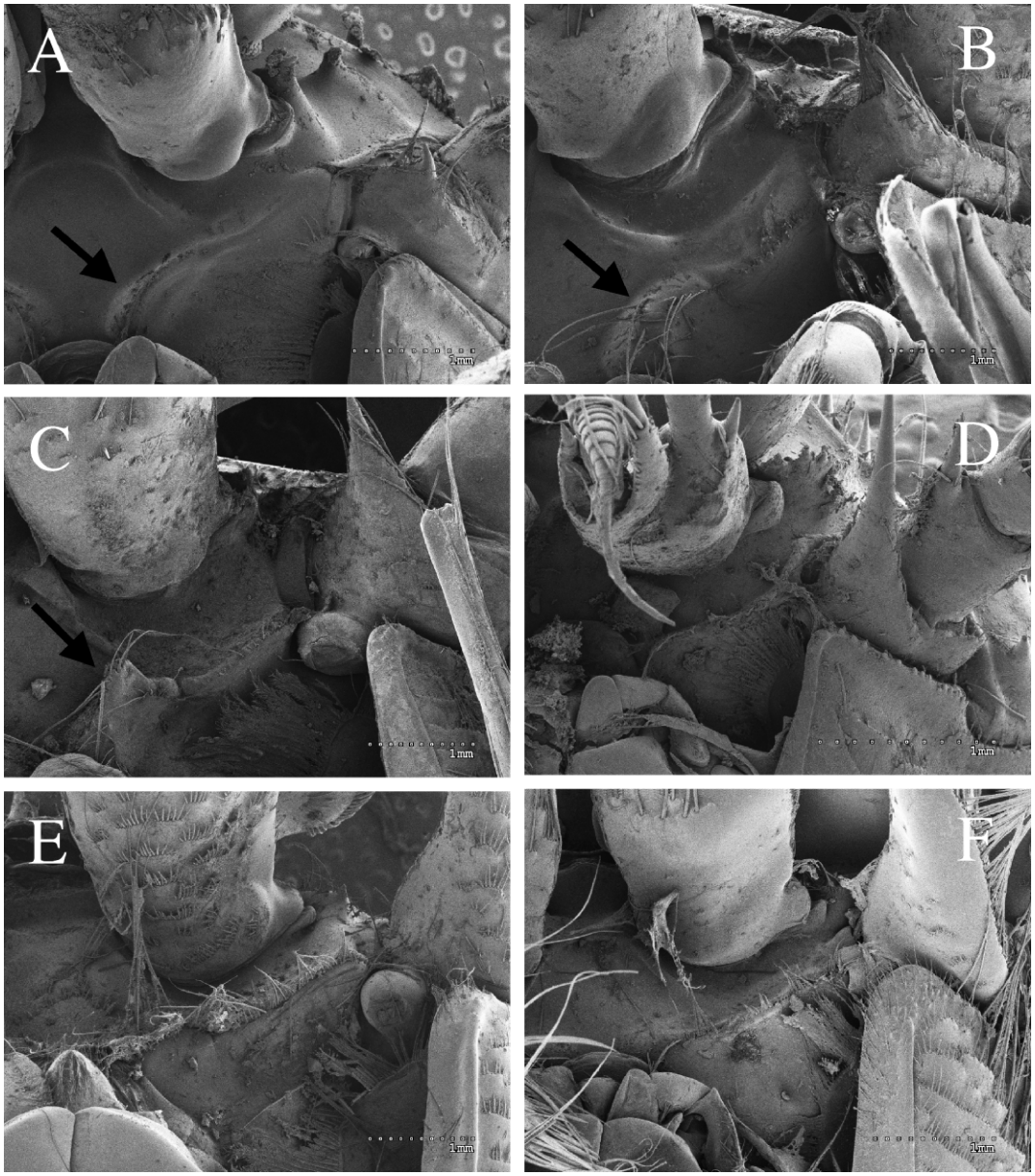


Fig. 3. Left antennule and antenna, including epistome. A, *Babamunida callista* F, 11.2 mm CL, Solomon Islands, cruise Salomon 2, stn 2200. B, *Munida rugosa* M, 18.0 mm CL, NE Atlantic, Jean Charcot, stn 9. C, *M. rubridigitalis* ov. F, 15.4 mm CL, New Caledonia, cruise Biocal, stn 52. D, *Raymunida cagnetei* M, 6.6 mm CL, French Polynesia, Marquesas Islands cruise Musorstom 9, stn 1177. E, *Agononida incerta* M, 15.2 mm CL, Indonesia, Kei Islands, cruise Karubar, stn 33. F, *Paramunida scabra* M, 12.3 mm CL, Indonesia, Kei Islands, cruise Karubar, stn 86. The arrows point out the direction of the lateral ridge. In *Babamunida* the lateral ridge ends between the antennular and antennal peduncles, and in *M. rugosa* and *M. rubridigitalis* it ends at the base of antennal segment.

Relationships between *Munida rugosa* and the other members of the genus *Munida* were not supported as a monophyletic cluster. Our 16S rRNA analysis indicated clear genetic differentiation between the specimens of *Munida* from the South Western Pacific previously analysed in Machordom and Macpherson (2004), and the type species, *Munida rugosa* from the North Eastern Atlantic Ocean. Thus, a molecular study including more species of the genus *Munida* from the Atlantic, should clarify the taxonomic and phylogenetic position of the genus between

←

Fig. 2. Bayesian tree based on 16S rRNA gene sequences, showing phylogenetic relationships among *Babamunida* and related genera. Numbers above branches indicate posterior probabilities (Pp $\geq$ 80) and bootstrap values (Bv $\geq$ 50) for NJ. Numbers below branches indicate consensus values (Cv $\geq$ 95) for the MP and bootstrap values (Bv $\geq$ 50) for ML.

the two regions (D. Bailie, University of Belfast, in preparation).

The poor resolution of the relationships among the main genera could be a consequence of the rapid radiation of species of *Munida* and related genera suggested by Machordom and Macpherson (2004). Nevertheless, the use of nuclear and more conserved genes, such as the 18S rRNA gene, could help resolve relationships at the deepest nodes. Because of its slow evolution rate, this gene seems to be particularly useful for resolving phylogenetic relationships among crustaceans at the higher taxonomic levels (Spears et al., 1992; Harris et al., 2000; Macpherson et al., 2005).

The genetic relationships observed within the new genus indicated two differentiated groups, *B. callista-B. plexaura*, and *B. hystrix-B. javieri*. Intrageneric distances among them are fairly high, but within the range cited for other decapod taxa (Harrison and Crespi, 1999; Ptacek et al., 2001; Harrison, 2004). This high level of genetic divergence contrasts with the scarce number of morphological characters that differentiate the species (see Macpherson and de Saint Laurent, 1991; Macpherson, 1994). This feature, however, is not rare in crabs or squat lobsters, in which convergence in the adult form and cryptic speciation appears common (Baldwin et al., 1998; Harrison and Crespi, 1999; Macpherson and Machordom, 2005; Mathews, 2006). This intense stasis or convergence in morphological characters could be due to ecological characters or to certain morphological constraints that might be especially strong in these organisms.

The species of *Babamunida* also share several ecological characteristics. All species have conspicuous colour bands (yellow, purple or red) on the body and appendages and live in waters with hard bottoms, with numerous corals and sponges. The depth ranges of the species are: 37-119 m (*B. brucei*), 327-590 m (*B. callista*), 100-300 m (*B. hystrix*), 280-460 m (*B. javieri*), and 110-540 m (*B. plexaura*).

The combination of molecular and morphological information has proven to be very useful for resolving the phylogenetic relationships in this group, and emphasizes the importance of subtle characters of the adult and larval forms for the systematics of this genus.

Key to Species of the Genus *Babamunida*

1. Dorsal surface of carapace with numerous small spines on anterior half 2
— Dorsal surface of carapace with row of epigastric spines and 1 parahepatic spine on each side of the anterior half 3
2. Cheliped fingers more than 2.5 times as long as palm. Antennular basal article with distomesial spine as long as distolateral spine . . . . . *B. brucei*
— Cheliped fingers barely 2 times as long as palm. Antennular basal article with distomesial spine shorter than distolateral spine . . . . . *B. hystrix*
3. Whole posterior margin of third sternite contiguous to fourth sternite . . . . . *B. javieri*
— Median part of third sternite contiguous to fourth sternite 4
4. Carapace with numerous striae (ca. 14 on posterior half, including interrupted striae). Anterolateral spine of carapace reaching the level of the sinus between rostral and supraocular spines. Carpus of first walking leg with 1 spine on dorsal crest. . . . . *B. callista*
— Carapace with moderately dense striae (ca. 10 on posterior half, including interrupted striae). Anterolateral spine of carapace falling short of level of the sinus between rostral and supraocular spines. Carpus of first walking leg with 3 spines on dorsal crest. . . . . *B. plexaura*

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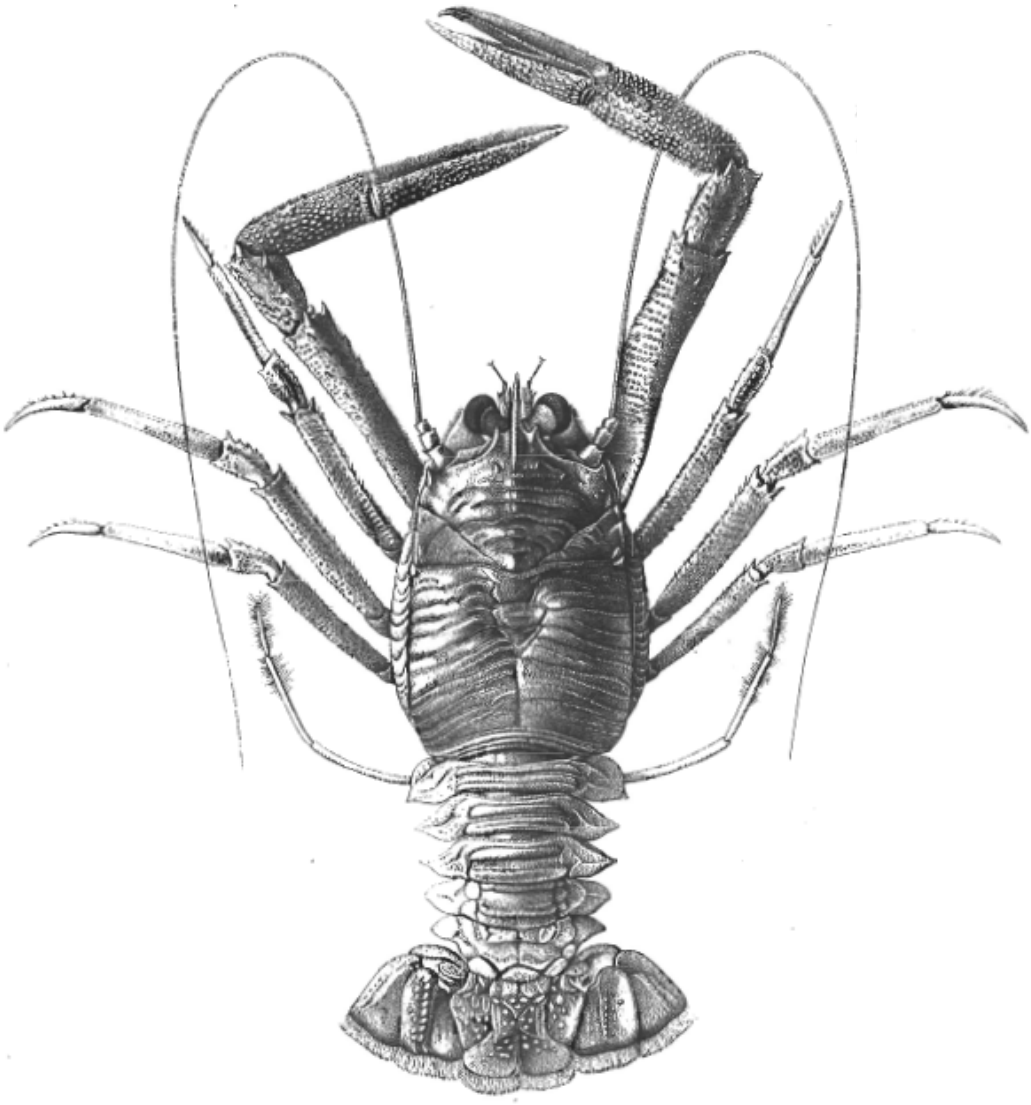

Pleuroncodes monodon (H. Milne Edwards, 1837)

CAPÍTULO II

Zoological Journal of the Linnean Society, 2009, **156**, 465–493. With 11 figures

Morphological and molecular description of new species of squat lobster (Crustacea: Decapoda: Galatheidae) from the Solomon and Fiji Islands (South-West Pacific)

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The family Galatheidae is among the most diverse families of anomuran decapod crustaceans, and the South-West Pacific is a biodiversity hot spot for these squat lobsters. Attempts to clarify the taxonomic and evolutionary relationships of the Galatheidae on the basis of morphological and molecular data have revealed the existence of several cryptic species, differentiated only by subtle morphological characters. Despite these efforts, however, relationships among genera are poorly understood, and the family is in need of a detailed systematic review. In this study, we assess material collected in different surveys conducted in the Solomon Islands, as well as comparative material from the Fiji Islands, by examining both the morphology of the specimens and two mitochondrial markers (cytochrome oxidase subunit I, COI, and 16S rRNA). These two sources of data revealed the existence of eight new species of squat lobster, four of which were ascribed to the genus *Munida*, two to the genus *Paramunida*, one to the genus *Plesionida*, and the last species was ascribed to the genus *Agononida*. These eight species are described along with phylogenetic relationships at the genus level. Our findings support the taxonomic status of the new species, yet the phylogenetic relationships are not yet fully resolved. Further molecular analysis of a larger data set of species, and more conserved genes, will help clarify the systematics of this group. *Zoological Journal of the Linnean Society*, 2009, **156**, 465–493.

ADDITIONAL KEYWORDS: 16S rRNA gene – COI gene – decapoda – molecular systematics – morphology.

INTRODUCTION

Squat lobsters of the family Galatheidae Samouelle, 1819 are among the most diverse families of anomuran decapod crustaceans, and their distribution includes all marine habitats, except polar regions, with a hot-spot of biodiversity in the Indo-West Pacific (Baba, 2005). This area has received the greatest taxonomic attention in the last few decades (Baba, 1988; Macpherson, 1994; Baba, 2005; Macpherson & Baba, 2006; Macpherson, 2006a), and numerous new species have been described as a result of the large sampling effort. At present, the family contains 33 genera, with the most widely represented decapod taxa in these waters being ascribed to the genus *Munida* Leach, 1820 and closely related genera. In effect, more than 250 species of these genera have been cited for the area (Baba, 2005, and references cited therein). Despite the fact that the galatheoid fauna is well known in many areas of the South-West Pacific, e.g. New Caledonia (Macpherson, 1994, 1996, 2006b), Fiji and Tonga (Baba, 1995); (Macpherson, 2004), eastern Australia (Ahyong & Poore, 2004), and New Zealand (Ahyong, 2007), this biota has been barely studied in the Solomon Islands. Most studies carried out in the waters of the Solomon Islands have focused on shallow waters (Challis, 1969; Miller,

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1969; Wolff, 1969; Bruce, 1980; Blaber & Milton, 1990), and those examining deep-sea faunas (Macpherson, 2003; Goggin, 2004; Castro, 2005; Ahyong & Galil, 2006; Cleva & Crosnier, 2006; Galil, 2007) have provided no information on galatheoid fauna.

The evolution of these squat lobsters seems to be marked by rapid speciation, and stasis during the Miocene, with some genera (e.g. *Munida*, *Paramunida*, and *Raymunida*) being monophyletic, according to both morphological and molecular data, and others (e.g. *Agononida* and *Crosnierita*) appearing as poly- or paraphyletic (Machordom & Macpherson, 2004). Knowledge of the phylogeny of the group is still scarce, and more data are needed to clarify the taxonomy and evolution of the different genera. Here, we describe a number of new species of the genera *Agononida*, *Munida*, *Paramunida*, and *Plesionida* for the area, based on both morphological and molecular information. This was necessary because diagnostic characters in the family Galatheidae and other decapod families are often based on subtle morphological differences. The use of additional information sources, such as molecular tools, is therefore strongly recommended. We selected two mitochondrial markers, the cytochrome oxidase subunit I (COI) gene and the 16S rRNA gene. These genes have been previously used to elucidate phylogenetic relationships at the genus and species level in this family (Lin, Chan & Chu, 2004; Cubelio *et al.*, 2007; Cabezas, Macpherson & Machordom, 2008), and in other decapod crustaceans, such as the family Palinuridae (Groeneveld *et al.*, 2007).

We examined specimens of the family Galatheidae collected during expeditions to the Solomon Islands (designated SALOMON 1 and SALOMON 2), and also re-examined material collected in surveys conducted in Fiji (MUSORSTOM 10 and BORDAU 1) and in New Caledonia (HALIPRO 1, HALIPRO 2 and BATHUS 1). This work represents the first record of the genera *Munida*, *Paramunida*, *Plesionida* and *Agononida* for the Solomon Islands.

Here, we describe and illustrate seven new species from the Solomon Islands: one species belonging to the genus *Agononida*, one to the genus *Plesionida*, two to the genus *Paramunida*, and three to *Munida*. A further species ascribed to the genus *Munida*, closely related to one of the above new species, is described for the region of Fiji. Molecular data are used to increase the knowledge on the phylogenetic relationships of the genera. Both the morphological and molecular data support the taxonomic status of the new species.

MATERIAL AND METHODS

Sampling and identification

Specimens were collected using beam trawls or Waren dredges in expeditions to the Solomon Islands conducted in September–October 2001 (SALOMON 1) and October–November 2004 (SALOMON 2). For comparative purposes, we also examined some specimens from Fiji and New Caledonia (Table 1). The material examined was deposited in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN). Measurements of specimens represent the postorbital carapace length. The terminology used mainly follows Zariquiey Alvarez (1952), Baba & de Saint Laurent (1996) and Baba (2005). Following Baba (2005), the terms flexor and extensor borders of

Table 1. Squat lobster species examined genetically, and the corresponding sample size, locality, station, depth, and survey label

Species	*N*	Locality	Station	Depth (m)	Survey
***Agononida isabelensis* sp. nov.**	2	Solomon Islands	Stn 2210	240–347	SALOMON 2
***Paramunida lophia* sp. nov.**	3	Solomon Islands	Stn 1831/2199	135–325	SALOMON 1/2
***Paramunida salai* sp. nov.**	3	Solomon Islands	Stn 1831	135–325	SALOMON 1
Paramunida proxima	1	Solomon Islands	Stn 1831	135–325	SALOMON 1
Paramunida stichas	2	Solomon Islands	Stn 1831	135–325	SALOMON 1
***Plesionida concava* sp. nov.**	2	Solomon Islands	Stn 2260	399–427	SALOMON 2
***Munida oblongata* sp. nov.**	1	Solomon Islands	Stn 2297	728–777	SALOMON 2
***Munida mendagnai* sp. nov.**	2	Solomon Islands	Stn 1825/1826	340–432	SALOMON 1
***Munida caeli* sp. nov.**	2	Solomon Islands	Stn 1801/1802	245–271	SALOMON 1
Munida delicata	1	Solomon Islands	Stn 2263	485–520	SALOMON 2
Munida leagora	2	Solomon Islands	Stn 2202	304–395	SALOMON 2
***Munida lailai* sp. nov.**	1	Fiji Islands	Stn 1348	327–420	MUSORSTOM 10/BORDAU 1
Munida parca	2	New Caledonia	Stn 687/851	314–440	BATHUS 1/HALIPRO 1
Munida devestiva	1	New Caledonia	Stn 60	1133–1280	HALIPRO 2

articles are only used for the maxilipeds and dactyli of the walking legs. The abbreviations used in the text are as follows: F, female; juv., juvenile; M, male; Mxp, maxiliped; ovig., ovigerous; P1, pereiopod 1, cheliped; P2–P4, pereiopods 2–4, first to third walking legs.

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from tissue samples using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen). Fragments of the COI and 16S rRNA genes were amplified by polymerase chain reaction (PCR). Primers used for the amplification of COI were COIH (Machordom & Macpherson, 2004), six bases shorter than HCO2198 from Folmer *et al.* (1994), and the newly designed primers ParaCOIF 5′-GGMGC HTGRGCHGGHATAG-3′ and ParaCOIR1 5′-GGRTC TCCWCCWCCDGCRGGRTC-3′. Unfortunately, some specimens belonging to the genus *Munida* yielded no results in the COI amplification. The 16S rRNA fragment was amplified using the primers L12 5′-TGA CCGTGCAAAGGTAGCATAA-3′ (Schubart, Diesel & Hedges, 1998) and 16SBR 5′-CCGGTCTGAACTCAG ATCACGT-3′ (Palumbi *et al.*, 1991).

Reactions were prepared in a final volume of 50 μL, and the PCR mix contained 2 μL of DNA template, 0.16 μM of both primers, 0.2 mM of each deoxyribonucleotide triphosphate (dNTP), 5 μL of buffer (containing a final concentration of 2 mM $MgCl_2$), 0.5 μL of bovine serum albumin (BSA; 10 mg mL^{-1}), 1.5 U of Taq DNA polymerase (Biotools) and double-distilled water (ddH_2O). The amplification process for the 16S rRNA sequence was conducted as follows: 94 °C (4 min), 40 cycles at 94 °C (45 s), 45 °C (1 min), 72 °C (1 min), and a final extension at 72 °C (10 min). Amplification of the COI gene was performed under the same conditions, except for a higher annealing temperature (50 °C).

The amplified fragments, 526 bp for the 16S rRNA gene and 657 bp for the COI gene, after removing primer regions, were purified by ethanol precipitation prior to sequencing both strands using 'Big Dye Terminator' (Applied Biosystems, ABI). Sequences were run on an ABI 3730 Genetic Analyzer (Applied Biosystems). Forward and reverse DNA sequence strands were compared using the Sequencher program (Gene Code) after removing the primer regions. New sequences were deposited in GenBank under accession numbers EU417965–EU418012.

PHYLOGENETIC ANALYSES

The 16S rRNA and COI sequences were checked using the program Sequencher (Gene Code), and alignment was performed by hand using the program PAUP* v4.0 b10 (Swofford, 2002). All analyses were performed separately for each of the genera *Agononida*, *Munida*, and *Paramunida* (except for the genus *Plesionida*, which was jointly analysed with the genus *Paramunida*, as only two species of the genus were examined). The evolutionary molecular model that best fitted our data was selected using ModelTest 3.7 (Posada & Crandall, 1998) and the Akaike's Information Criterion (Akaike, 1974). Phylogenetic analyses were conducted for each gene data set, and for the combined data set, using the following software: MrBayes v3.0B4 (Huelsenbeck & Ronquist, 2001) for Bayesian analyses (MB), PAUP* v4.0 b10 (Swofford, 2002) for neighbour-joining (NJ) and maximum-parsimony (MP) analyses, and PhyML v2.4.4 (Guindon & Gascuel, 2003) for maximum-likelihood analyses (ML). Firstly, analyses were performed for 16S rRNA and COI separately, and secondly the incongruence length differences test (Mickevich & Farris, 1981; Farris *et al.*, 1994) was used to test phylogenetic congruence between the two analysed regions, and treated both genes together (homogeneity partition test in PAUP* v4.0 b10). The MP analyses were performed through a heuristic search with the tree bisection and reconnection (TBR) algorithm, with simple step-wise addition, and treating indels as a fifth state. The ML analyses were conducted in Phyml v2.4.4 using the model selected by ModelTest 3.7, and allowing the program to estimate the model parameters. Not all of the models from ModelTest 3.7 are implemented in PhyML v2.4.4; therefore, when the best-fitting model selected was not implemented, the second one was used in the ML analyses, as recommended by the authors.

We estimated support in different analyses by bootstrapping (Felsenstein, 1985): NJ (2000 pseudoreplicates), ML (500 pseudoreplications), and MP (1000 pseudoreplicates). For the Bayesian analyses, four chains were run for 5 000 000 generations, with a sample frequency of 100. Trees prior to the log likelihood stabilization tree were discarded as burn-in. The first 5000 trees were discarded in the analyses for the genera *Paramunida* and *Plesionida*, and the first 10 000 were discarded for the genera *Agononida* and *Munida*, such that 45 000 and 40 000 trees were computed for the consensus tree. Robustness of the inferred trees was evaluated through Bayesian posterior probabilities (BPPs).

RESULTS

SYSTEMATICS

AGONONIDA ISABELENSIS SP. NOV. (FIG. 1)

Material examined: Solomon Islands. SALOMON 1. Stn 1801, 09°25.0′S, 160°25.9′E, 1 October 2001, 254–271 m: 1 M, 20.7 mm (holotype, MNHN-Ga6496);

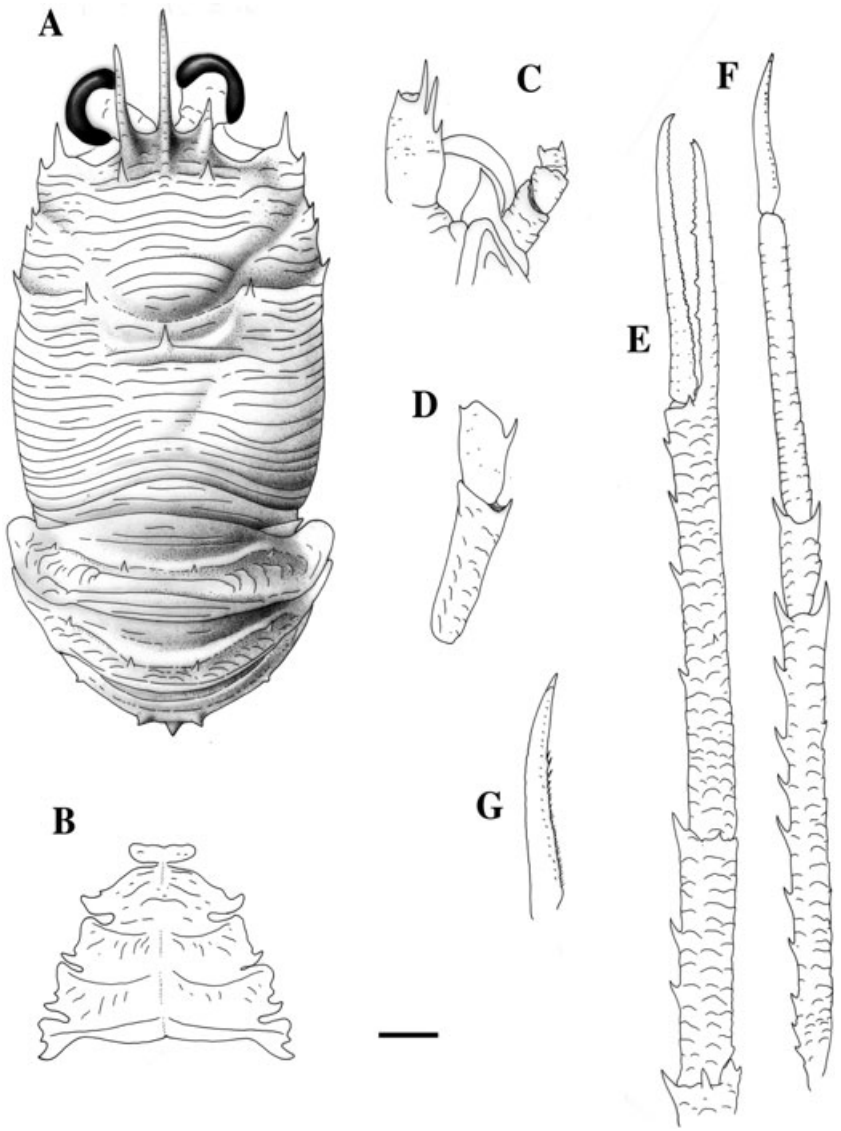

Figure 1. ***Agononida isabelensis*** **sp. nov.** male holotype, 20.7 mm (MNHN-Ga 6496), Solomon Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, right P2, lateral view. G, dactylus, right P2, lateral view. Scale: A, B, E, F = 5 mm; C, D, G = 2 mm.

3 M, 14.0–20.7 mm; 3 ov. F, 17.2–18.4 mm (paratypes, MNHN-Ga6497). Stn 1802, 09°31.1′S, 160°35.0′E, 2 October 2001, 245–269 m: 2 M, 14.0–14.4 mm (paratypes, MNHN-Ga6498). Stn 1803, 09°32.1′S, 160°37.3′E, 2 October 2001, 308–347 m: 1 M 17.6 mm (paratype, MNHN-Ga6499). Stn 1860, 09°22′S, 160°31′E, 7 October 2001, 620 m: 5 M, 6.8–16.0 mm; 3 F, 7.2–14.4 mm (paratype, MNHN-Ga6500).

SALOMON 2. Stn 2210, 07°33.5′S, 157°42.3′E, 26 October 2004, 240–305 m: 11 M, 6.9–19.0 mm; 3 ov. F, 14.1–15.1 mm; 3 F, 9.4–11.5 mm (paratypes MNHN-Ga6501). Stn 2287, 8°39.84′S, 157°23.505′E, 6 November 2004, 253–255 m: 2 juv., 5.3–5.5 mm (paratypes, MNHN-Ga6502).

Etymology: From *Isabel*, one of the Solomon Islands from which some of the specimens were collected.

Description: Carapace as long as wide. Transverse ridges usually interrupted in cardiac and branchial regions by dense, short non-iridescent setae. Gastric region with two epigastric spines; one median cardiac spine and one postcervical spine on each side. Posterior border of carapace unarmed. Frontal margins transverse, slightly concave. Lateral margins slightly convex. Anterolateral spine strong at anterolateral angle, reaching or overreaching the level of the sinus between the rostrum and the supraocular spines. Second marginal spine before cervical groove 0.3 of

the preceding one. Branchial margins with three spines. Rostrum spiniform, nearly half as long as remaining carapace, straight, and horizontal. Supraocular spines (right spine regenerating in holotype) slightly thicker than rostral spine, clearly overreaching midlength of rostrum, and exceeding ends of corneas, slightly divergent, directed slightly upwards (Fig. 1A).

Thoracic sternites with numerous short striae. Anterior part of fourth sternite slightly narrower than third; median part of posterior margin of third sternite contiguous to fourth sternite. Transverse ridges between fifth, sixth, and seventh sternites obtuse, feebly granulated (Fig. 1B).

Second to fourth abdominal somites with four spines on anterior ridge, with some transverse striae and scales. Posterior ridge of fourth abdominal somite bears median spine.

Eyes large: maximum corneal diameter 0.3 times the distance between the bases of the anterolateral spines.

Basal segments of antennule (distal spines excluded) about 0.3 times the carapace length, elongate, overreaching corneae, with two distal spines, mesial spine clearly shorter than lateral spine; with two spines on lateral margin, proximal spine short, distal spine moderately long (Fig. 1C). First segment of antennal peduncle with stout process on mesial margin reaching end of second segment; second to fourth segments unarmed (Fig. 1C).

With Mxp 3 ischium about twice the length of the merus, measured along the dorsal margin, and distoventrally bearing a long spine. Merus with one well-developed median spine on flexor margin; extensor margin with small distal spine (Fig. 1D).

With P1s subequal in length, squamous, with some uniramous and plumose setae, and with some iridescent setae on mesial borders of merus and carpus, about five times the carapace length; merus clearly longer than carapace length, carpus four times longer than high, and 0.7 times palm length; palm nearly nine times longer than high, and 1.4 times longer than fingers. Merus armed with row of spines on mesial, ventral, and dorsal borders. Carpus and palm with row of spines on mesial margin, a few small spines on dorsal side. Fingers unarmed, with longitudinal carina on each side, distally curving and crossing, and ending in a sharp point (fixed finger of right cheliped in holotype regenerating) (Fig. 1E).

With P2 about three times the carapace length; merus nearly 1.5 times longer than carapace, between nine and ten times as long as high, 4.0–4.5 times the carpus length, and 1.3–1.5 times as long as propodus; propodus ten times as long as high, and nearly twice the dactylus length (Fig. 1F); end of propodus reaching or slightly overreaching end of P1 merus. Merus with spines along dorsal border, increasing in size distally, a few small spines along distal part of ventral margin, with distal spine strong. Carpus with strong distomesial and distoventral spine. Propodus with row of minute movable small ventral spinules (not discernible in Fig. 1F). Dactylus slightly curving distally, ventral margin slightly curving with 26–28 movable small spinules, distal third unarmed (Fig. 1F, G). Length, armature, and article proportions of P3 and P4 similar to those of P2.

Remarks: The new species closely resembles *Agononida prolixa* (Alcock, 1894) from the Arabian Sea, Sri Lanka, and the Andaman Sea (Ahyong & Poore, 2004; Baba, 2005). In both species, supraocular spines fall short of the rostral tip, the carapace has three branchial lateral spines, protogastric spines are absent, the fourth abdominal segment has one spine on the posterior transverse ridge, and the basal article of the antennal peduncle bears a moderately sized process, not overreaching the fourth article.

The two species may be distinguished as follows.

1. The posterior margin of the carapace is armed with two median spines in *A. prolixa*, whereas these spines are absent in the new species.
2. The distomesial angle of the second article of the antennal peduncle is armed with a spine in *A. prolixa*. In *A. isabelensis* sp. nov., this angle is unarmed.

The new species is also close to *Agononida similis* (Baba, 1988) from the Philippines and Indonesia (Baba, 1988). However, they can be differentiated according to the number of spines along the branchial margin of the carapace: four in *A. similis* and three in *A. isabelensis* sp. nov. Furthermore, the lateral margin of the basal article of the antennular peduncle has two well-developed spines in the new species, whereas this margin has only one spine in *A. similis*.

Distribution: Solomon Islands, at a depth of between 240 and 347 m.

MUNIDA CAELI SP. NOV. (FIG. 2)

Material examined: Solomon Islands. SALOMON 1. Stn 1801, 09°25.0′S, 160°25.9′E, 1 October 2001, 254–271 m: 1 M, 6.5 mm; 1 ov. F, 5.8 mm (paratype, MNHN-Ga6503). Stn 1802, 09°31.1′S, 160°35.0′E, 2 October 2001, 245–269 m: 1 M, 6.2 mm (paratype, MNHN-Ga6504); 1 ov. F, 6.0 mm (holotype, MNHN-Ga6505).

Etymology: The name *caeli* refers to one of the southern hemisphere constellations (the Graving Tool).

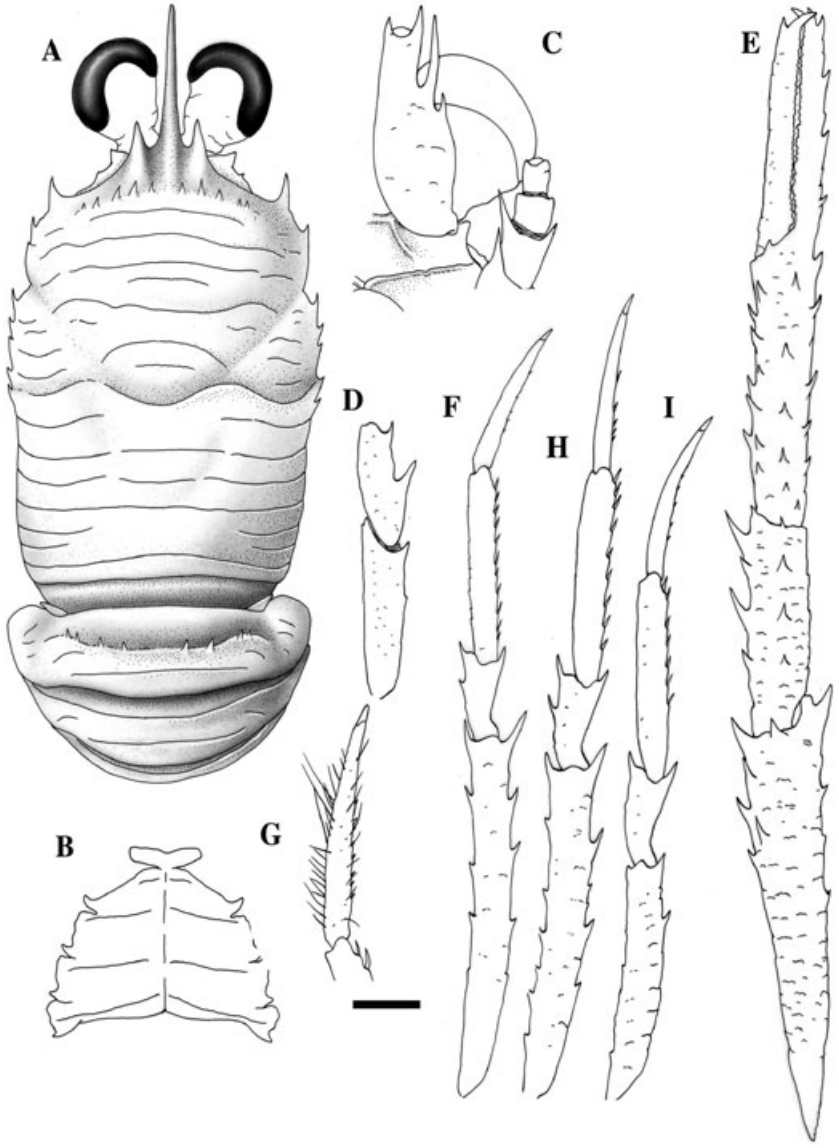

Figure 2. ***Munida caeli*** **sp. nov.**, ovigerous female holotype, 6.0 mm (MNHN Ga6505). Solomon Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, right P2, lateral view. G, dactylus, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, B, E, F, H, I = 1 mm; C, D, G = 0.5 mm.

Description: Carapace 1.2 times longer than wide, slightly convex dorsally. Transverse ridges mostly interrupted by dense short, non-iridescent setae. Intestinal region without striae or scales. Few scales, and secondary striae between main striae. Gastric region with a row of ten epigastric spines, other regions unarmed. Frontal margins slightly oblique. Lateral margins feebly convex. Anterolateral spine well-developed, situated at anterolateral angle, clearly not reaching the level of the sinus between the rostrum and the supraocular spines. Second marginal spine before cervical groove small, three times smaller than the preceding one. Branchial margins with five small spines, decreasing in size posteriorly. Rostrum spiniform, nearly half as long as remaining carapace, slightly curved. Supraocular spines short, not reaching midlength of rostrum, and clearly not exceeding ends of corneas, subparallel, upwardly directed (Fig. 2A).

Fourth thoracic sternite with a few small scales; lateral surface of fifth to seventh sternites smooth. Anterior part of fourth sternite narrower than third, slightly concave medially; median posterior margin of third sternite contiguous with fourth sternite.

Transverse ridges between fifth, sixth, and seventh sternites obtuse, feebly granulated (Fig. 2B).

Second abdominal tergite with eight spines on anterior ridge. Second and third tergites each with one transverse continuous stria.

Epistome crest without hump near mouth opening.

Eyes moderately large: maximum corneal diameter nearly half of the distance between the bases of the anterolateral spines.

Basal segment of antennule (distal spines excluded) about 0.25 times the carapace length, elongate, ending at the same level or slightly exceeding the corneas, with two distal spines, and with mesial spine shorter than lateral spine; two spines on lateral margin, proximal one short, located at midlength of segment, distal one long, nearly reaching end of distolateral spine (Fig. 2C). First segment of antennal peduncle with one distal spine on mesial margin, reaching end of second segment; second segment with two distal spines, mesial spine clearly longer than lateral spine, reaching end of third segment; third segment unarmed (Fig. 2C).

With Mxp 3 ischium nearly twice the length of the merus, measured along the dorsal margin, and distoventrally bearing a spine. Merus bearing two spines on flexor margin, proximal spine longer than distal spine; extensor margin unarmed (Fig. 2D).

With P1 squamate, three times the carapace length, with a few uniramous setae on the mesial borders of articles. Merus as long as carapace, nearly twice the carpus length, armed with some spines, and with stronger spines on distal border, not reaching proximal fourth of carpus. Carpus 3.5–4.5 times longer than high, shorter than hand, with a few strong spines on the mesial margin, and some short spines on the dorsal side. Palm as long as fingers, with row of spines along mesial and lateral borders, and some small spines on dorsal side. Fingers distally curving and crossing, and ending in a sharp point; fixed finger with some spines along entire border, with two distal spines, and ending in sharp point; movable finger unarmed, except for terminal spine (Fig. 2E).

With P2 twice the carapace length; merus slightly shorter than carapace, about 8–11 times as long as high, between four and five times the carpus length, and twice the propodus length; propodus between six and eight times as long as high, and 1.1–1.5 times longer than dactylus (Fig. 2F). Merus with row of some spines along dorsal and ventral borders. Carpus with several dorsal spines and one distoventral spine; end of carpus nearly reaching level of the merocarpal articulation of P1. Propodus with 9–12 movable ventral spinules. Dactylus long and slender, with dorsal margin slightly convex on proximal half, slightly curving distally with seven or eight movable spinules along ventral margin, distal third unarmed (Fig. 2G). P3 similar in length and armature to P2; P3 merus slightly shorter than P2 merus, and P3 propodus slightly longer than P2 propodus (Fig. 2H). P4 shorter than P2 and P3; P4 merus about 0.6 times P2 merus (Fig. 2I); merocarpal articulation reaching level of anterolateral spine of carapace.

Remarks: The new species resembles *Munida parca* Macpherson, 1996 from New Caledonia, and *Munida lailai* sp. nov. from Fiji (see below), in that it has five spines on the lateral margin of the carapace behind the cervical groove, eyes moderately large, the second abdominal segment with spines, lateral sections of the posterior thoracic sternites without granules, rostrum spiniform, the distomesial spine of the basal antennular segment clearly shorter than the distolateral spine, the distomesial spine of the second antennal article reaching the end of the third article, and with the distal half of the ventral border of the dactylus unarmed. The species can be easily distinguished from *M. parca* according to the following characters.

1. The antennular peduncle is longer in *M. parca* than in *M. caeli* sp. nov. The basal article is very long and clearly exceeds the corneae in *M. parca*, whereas this article only ends or slightly exceeds the corneae in the new species.
2. The distomesial spine of the second antennal segment exceeds the third segment in the new species, whereas this spine is shorter in *M. parca*, and falls short of the distal margin of the third segment.
3. The chelipeds (P1) are more elongate in the new species, with the carpus being 3.5–4.5 times longer than broad, whereas the carpus is twice as long as it is broad in *M. parca*.

Munida caeli sp. nov. is also closely related to *M. lailai* sp. nov. (see the differences under the Remarks section of *M. lailai* sp. nov.).

Distribution: Solomon Islands, at a depth of between 245 and 271 m.

MUNIDA LAILAI SP. NOV. (FIG. 3)

Munida parca Macpherson, 2004: 271.

Material examined: Fiji Islands. MUSORSTOM 10. Stn 1348, 17°30.29′S, 178°39.63′E, 11 August 1998, 353–390 m: 1 M, 5.9 mm (holotype, MNHN-Ga6506).

BORDAU 1. Stn 1450, 16°44.45′S, 179°58.50′E, 4 March 1999, 327–420 m: 1 F, 4.6 mm (paratype, MNHN-Ga6507).

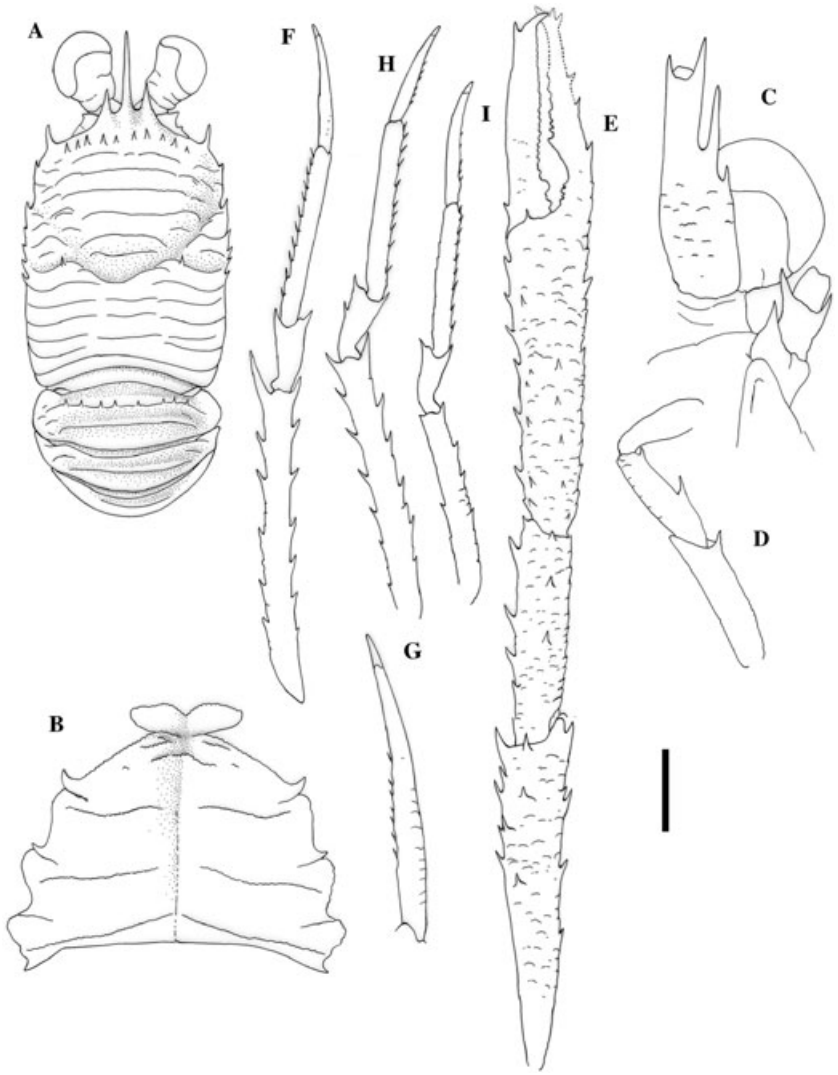

Figure 3. *Munida lailai* sp. nov., male holotype, 5.9 mm, (MNHN-Ga6506). Fiji Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, left P2, lateral view. G, dactylus, left P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, E, F, H, I = 2 mm; B, C, D, G = 1 mm.

Etymology: The name *lailai* means small in the Fijian language. The name may be considered as a noun in apposition.

Description: Carapace 1.2 times longer than wide. Transverse ridges usually interrupted in cardiac and branchial regions by very short, non-iridescent setae, and some scattered long iridescent setae. Intestinal region without scales. Dorsal surface of carapace armed with ten epigastric spines; one small postcervical spine on each side. Frontal margins slightly oblique. Lateral margins subparallel. Anterolateral spine well-developed, situated at anterolateral angle, clearly not reaching the level of the sinus between the rostrum and the supraocular spines. Second marginal spine before cervical groove small, about 0.25 times the length of the anterolateral spine. Branchial margins with five small spines. Rostrum spiniform, nearly 0.4 times the length of the remaining carapace, horizontal, carinated dorsally, and slightly convex. Supraocular spines short, not reaching midlength of rostrum, and clearly falling short of end of corneae, subparallel, slightly directed upwards (Fig. 3A).

Fourth thoracic sternite smooth, with a few short striae. Anterior section of fourth sternite narrower than third; median margin of third sternite contiguous with fourth sternite (Fig. 3B).

Second abdominal somite with eight spines along anterior ridge. Second and third somites each with one transverse stria.

Epistome crest without hump near mouth opening.

Eyes large: maximum corneal diameter 0.4 times the distance between the bases of the anterolateral spines.

Basal segment of antennule (distal spines excluded) about 0.4 times the carapace length, elongate, nearly three times longer than wide (excluding spines), overreaching end of corneae, with two distal spines, and with mesial spine clearly shorter than lateral spine; two spines on lateral margin, proximal one short, located at midlength of segment, distal one long, not reaching end of segment (excluding spines) (Fig. 3C). First segment of antennal peduncle with one short distomesial spine nearly reaching end of second segment; second segment with two distal spines, mesial spine slightly longer than lateral spine, not exceeding end of third segment; third segment unarmed (Fig. 3C).

With Mxp 3 ischium about 1.5 times the length of the merus, measured along the dorsal margin, and distoventrally bearing a spine. Merus of Mxp 3 with two well-developed spines on flexor margin, distal spine smaller; extensor margin unarmed (Fig. 3D).

With P1s subequal in length, about 4.5 times the carapace length, squamous, with numerous uniramous iridescent setae and plumose non-iridescent setae, denser on mesial and lateral borders of articles. Merus longer than carapace length, 1.5 times the carpus length, armed with some spines, with strongest spine on distal border, not reaching proximal fourth of carpus. Carpus four times as long as high, shorter than hand, several strong spines on mesial border, and some small spines on dorsal side. Palm 1.3 times longer than fingers, with row of mesial spines; some scattered small spines on dorsal side, and one row of lateral spines continuing onto fixed finger, and reaching tip. Movable finger unarmed, except proximal and distal spines. Fingers distally curving and crossing, ending in a sharp point, cutting edges slightly gaping in holotype (more straight in paratype), with small teeth of various sizes (Fig. 3E).

With P2 about three times the carapace length, with numerous uniramous iridescent setae and plumose non-iridescent setae along dorsal margins of articles; merus 1.3 times as long as carapace, about ten times as long as high, more than four times the carpus length, and 1.8 times as long as the propodus; propodus about nine times as long as high, and 1.3 times longer than dactylus (Fig. 3F). Dorsal border of merus with row of spines, increasing in size distally; ventral margin with row of spines, increasing in size distally. Carpus with distodorsal and distoventral spines; distal margin reaching the level of the merocarpal articulation of P1. Propodus with ten or 11 movable ventral spinules. Dactylus slightly curving distally, with seven movable spinules along ventral margin, and with distal third unarmed (Fig. 3G). P3 as long as P2; spination of P3 is similar to that of P2 (Fig. 3H). P4 length 0.8 times P2 length; merus 0.6 times the length of that of P2; spines along margins of merus and carpus less spinose than those of P2 and P3 (Fig. 3I); merocarpal articulation ending at the level of the anterolateral spine of the carapace.

Remarks: The new species is closely related to *M. parca* from New Caledonia (Macpherson, 1996) and *M. caeli* sp. nov. from the Solomon Islands (see above). The three species have five spines on the lateral margin of the carapace behind the cervical groove, eyes moderately large, the second abdominal segment with spines, the lateral portions of the posterior thoracic sternites without granules, rostrum spiniform, the epistome crest without a hump near the mouth opening, the distomesial spine of the basal antennular segment clearly shorter than the distolateral spine, and with the distomesial spine of the basal antennal article nearly reaching the end of the third article. *Munida lailai* sp. nov. can be distinguished from *M. parca* according to the following characters.

1. The chelipeds (P1) are clearly longer in the new species than in *M. parca*. In the new species, the length of P1 is about 4.5 times the carapace length, whereas this ratio is about 2.5 times in *M. parca*. The carpus is nearly 2.5 times longer than broad in *M. parca*, whereas it is four times longer than broad in the new species.
2. The walking legs (P2–P4) are longer in *M. parca*. P2 is about three times the carapace length in the new species, being slightly more than two times in *M. parca*. Furthermore, the merus of this leg is nearly as long as the carapace in *M. parca*, being longer in *M. lailai* sp. nov. In addition, the merocarpal articulation ends at the level of the anterolateral spine of the carapace in the new species, whereas in *M. parca* this articulation slightly exceeds the level of the anterior branch of the cervical groove.

On the other hand, *M. lailai* sp. nov. can be easily distinguished from *M. caeli* sp. nov. by the following aspects.

1. The antennular peduncle is clearly longer in *M. lailai* sp. nov. than in *M. caeli* sp. nov. The basal article clearly overreaches the corneae in *M. lailai* sp. nov., whereas this article only ends or slightly exceeds the corneae in *M. caeli* sp. nov.
2. The walking legs (P2–P4) are longer in *M. lailai* sp. nov. P2 is about three times the carapace length in *M. lailai* sp. nov., being twice the carapace length in *M. caeli* sp. nov.

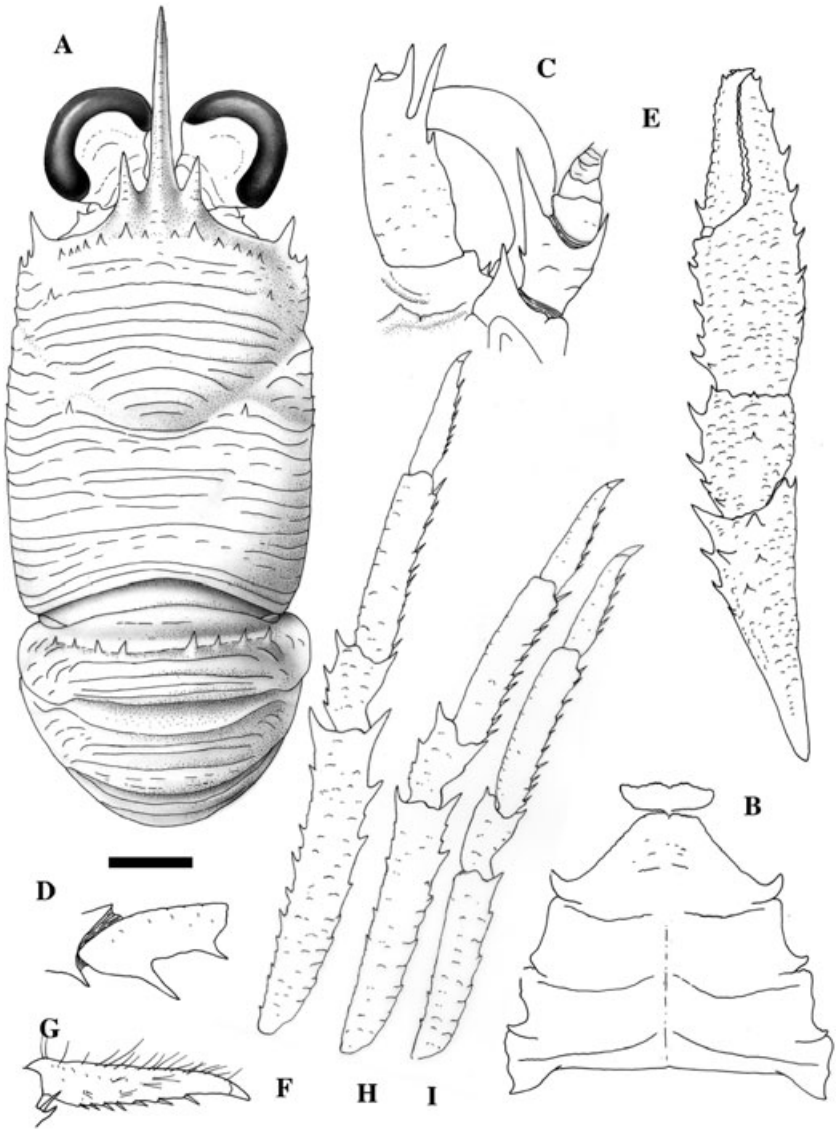

Figure 4. ***Munida mendagnai*** **sp. nov.**, male holotype, 7.3 mm (MNHN-Ga6510). Solomon Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, right P2, lateral view. G, dactylus, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, E, F, H, I = 1 mm; B, C, D, G = 0.5 mm.

Distribution: Fiji Islands, at a depth of between 327 and 420 m.

MUNIDA MENDAGNAI SP. NOV. (FIG. 4)

Material examined: Solomon Islands. SALOMON 1. Stn 1825, 09°50.5′S, 160°57.9′E, 4 October 2001, 340–391 m: 2 F, 7.1–7.2 mm (paratypes, MNHN-Ga6508). Stn 1826, 09°56.4′S, 161°03.9′E, 4 October 2004, 418–432 m: 1 M, 10.0 mm (paratype, MNHN-Ga6509); 1 M, 7.3 mm (holotype, MNHN-Ga6510).

Etymology: The name *mendagnai* is in honour of Alvaro de Mendaña, the Spanish explorer who named the Solomon Islands in 1568.

Description: Carapace 1.2 times longer than wide. Transverse ridges usually interrupted in cardiac and branchial regions by very short, non-iridescent setae, and by some scattered long iridescent setae. Small scales on intestinal region. Dorsal surface of carapace armed with 11–13 epigastric spines, one small hepatic, one parahepatic, and one postcervical spine on each side. Frontal margins transverse. Lateral margins subparallel. Anterolateral spine well-developed, situated at anterolateral angle, clearly not reaching the level of the sinus between the rostrum and the supraocular spines. Second marginal spine before cervical groove small, about 0.25 times the

length of the anterolateral spine. Branchial margins with five small spines. Rostrum spiniform, nearly 0.7 times the length of the remaining carapace, horizontal, dorsally carinated and slightly convex. Supraocular spines short, clearly not reaching the midlength of the rostrum, and not reaching the end of the corneae, subparallel, slightly directed upwards (Fig. 4A).

Fourth thoracic sternite smooth, with a few short striae. Anterior part of fourth sternite narrower than third; median margin of third sternite contiguous with fourth sternite (Fig. 4B).

Second abdominal somite with eight or nine spines along anterior ridge. Second and third somites each with between four and six transverse striae.

Epistome crest with hump near mouth opening.

Eyes large: maximum corneal diameter 0.5 times the distance between the bases of the anterolateral spines.

Basal segment of antennule (distal spines excluded) about 0.3 time the carapace length, elongate, about 2.5 times longer than wide (excluding spines), reaching end of corneae, with two distal spines, mesial spine shorter than lateral spine; two spines on lateral margin, proximal one short, located at midlength of segment, distal one long, reaching end of distal spines (Fig. 4C). First segment of antennal peduncle with one short distomesial spine nearly reaching the end of the second segment; second segment with two distal spines, mesial spine longer than lateral spine, slightly exceeding end of antennal peduncle, and with one additional mesial spine at midlength; third segment unarmed (Fig. 4C).

With Mxp 3 ischium about 1.5 times the length of the merus, measured along the dorsal margin, and distoventrally bearing a spine. Merus of Mxp 3 with two well-developed spines on flexor margin, distal margin smaller; extensor margin unarmed (Fig. 4D).

With P1s subequal in length, between 1.8 and 2.8 times the carapace length, squamous, with numerous uniramous iridescent setae and plumose non-iridescent setae, denser on mesial and lateral borders of articles. Merus shorter than carapace length, twice carpus length, armed with some spines, strongest spine on distal border, reaching proximal fourth of carpus. Carpus 1.4–1.7 times as long as high, shorter than hand, several strong spines on mesial border, and some small spines on dorsal side. Palm as long as fingers, with a row of mesial spines, with some scattered small spines on dorsal side, and one row of lateral spines continuing onto fixed finger and reaching tip. Movable finger unarmed, except proximal and distal spines. Fingers distally curving and crossing, ending in sharp points, cutting edges with small teeth of various sizes (Fig. 4E).

With P2 about twice the carapace length, with numerous uniramous iridescent setae and plumose non-iridescent setae along dorsal margins of articles; merus 0.8 times as long as carapace, between five and six times as long as high, 3.0–3.5 times the carpus length, and 1.5–1.8 times as long as the propodus; propodus between four and five times as long as high, and 1.2–1.3 times longer than dactylus (Fig. 4F). Dorsal border of merus with row of spines, increasing in size distally; ventral margin with row of spines, increasing in size distally. Carpus with several dorsal spines and one distoventral spine; distal margin clearly not reaching level of merocarpal articulation of P1. Propodus with between nine and 11 movable ventral spinules. Dactylus slightly curving distally, with seven movable spinules along ventral margin, distal fourth unarmed, ultimate spine clearly more remote from tip of dactylus than from penultimate spine (Fig. 4G). P3 0.9 times the length of P2; merus slightly shorter than that of P2; spination of P3 similar to that of P2 (Fig. 4H). P4 0.8 times the length of P2; merus 0.7 times the length of that of P2; spines along margins of merus and carpus less spinose than those of P2 and P3 (Fig. 4I); merocarpal articulation ending at the level of the anterior branch of the cervical groove.

Remarks: The new species is closely related to *Munida angusta* Macpherson, 2004 from the New Caledonia, Fiji, and Tonga islands (Macpherson, 2004). The two species have five spines on the lateral margin of the carapace behind the cervical groove, eyes large, the second abdominal segment with spines, lateral portions of the posterior thoracic sternites without granules, rostrum spiniform, the epistome crest with a hump near the mouth opening, the distomesial spine of the basal antennular segment clearly shorter than the distolateral spine, and the distomesial spine of the second antennal article reaching the end of the fourth article. The two species can be distinguished according to the following characters.

1. The second and third abdominal segments have between four and six transverse striae in the new species, instead of only one or two striae in *M. angusta*.
2. The chelipeds (P1) are clearly larger and shorter in the new species than in *M. angusta*. In the new species, the length of P1 is between 1.8 and 2.8 times the carapace length, whereas this ratio is between 3.0 and 4.5 times in *M. angusta*. The carpus is more than three times longer than broad in *M. angusta*, and 1.4–1.7 times longer than broad in the new species. The movable finger has a row of spines along the mesial margin in *M. angusta*, whereas this margin has only one proximal and one distal spine in the new species.

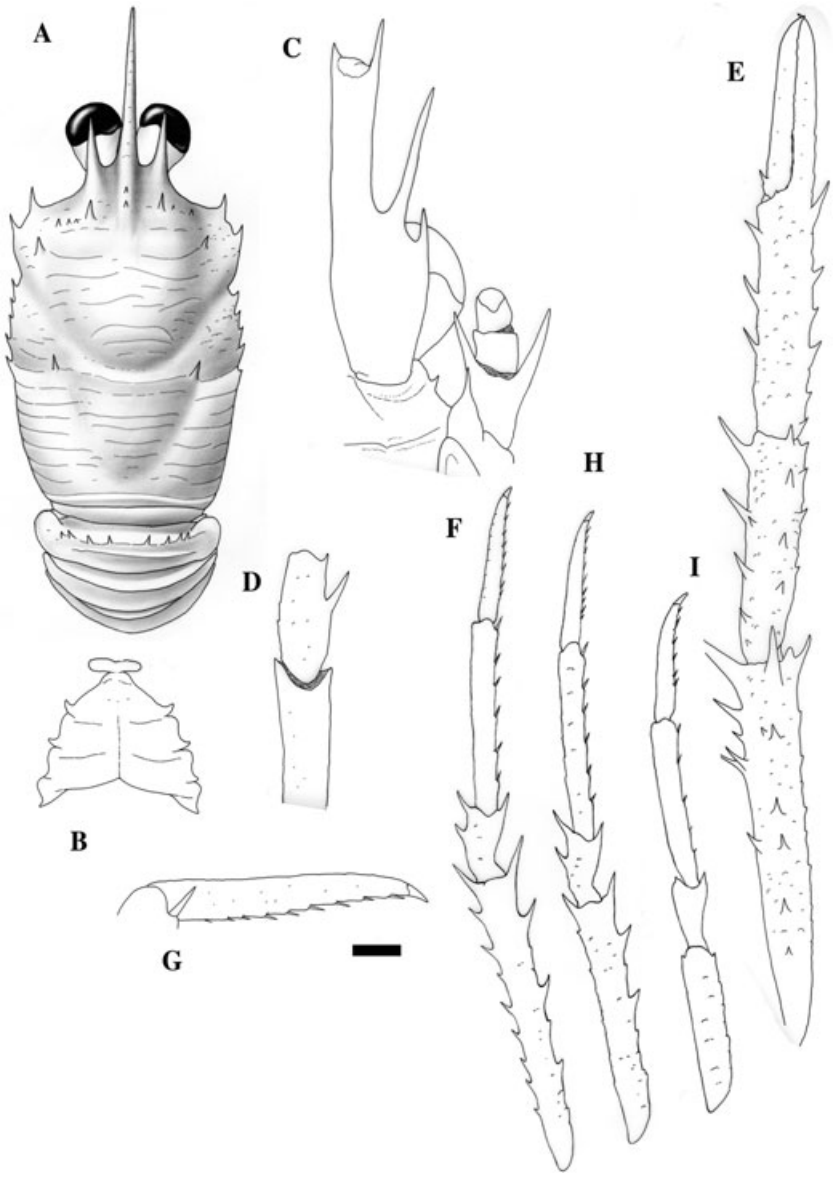

Figure 5. ***Munida oblongata*** **sp. nov.**, male holotype, 6.1 mm (MNHN-Ga6511). Solomon Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium, and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, right P2, lateral view. G, dactylus, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, B, E, F, H, I = 1 mm; C, D, G = 0.5 mm.

3. The walking legs (P2–P4) are longer and more slender in *M. angusta*. P2 is about 1.5 times the carapace length in the new species, being 2.5 times that in *M. angusta*. Furthermore, the length of the merus of this leg is 0.8 times the carapace length in *M. mendagnai* sp. nov., being 1.2 times that in *M. angusta*. Finally, the dactyli of the walking legs are very slender, with the distal third of the ventral border unarmed in *M. angusta*, whereas dactyli are stouter, and the distal fourth of their ventral borders are unarmed, in the new species.

Distribution: Solomon Islands, at a depth of between 340 and 432 m.

MUNIDA OBLONGATA SP. NOV. (FIG. 5)

Material examined: Solomon Islands. SALOMON 2. Stn 2297, 9°05.69′S, 158°14.82′E, 8 November 2004, 728–777 m: 1 M, 6.1 mm (holotype, MNHN-Ga6511).

Etymology: From the Latin, *oblongus*, meaning longer than broad, referring to the long and slender basal segment of the antennule.

Description: Carapace 1.2 times longer than wide. A few secondary striae between main transverse ridges. Ridges with very short non-iridescent setae. Gastric region with one pair of well-developed and two pairs of small epigastric spines. Usually one parahepatic spine and one postcervical spine on each side. Frontal margins almost transverse. Lateral margins slightly convex. Anterolateral spine moderately long, near anterolateral angle, not reaching the level of the sinus between the rostrum and the supraocular spines. Second marginal spine before cervical groove smaller than preceding one. Branchial margins with five spines. Rostrum spiniform, about 0.6 times as long as remaining carapace, straight, and horizontal. Supraocular spines reaching midlength of rostrum, and not reaching end of corneae, subparallel, directed slightly upwards (Fig. 5A). Thoracic sternites smooth. Anterior margin of fourth sternite clearly narrower than third (Fig. 5B).

Second abdominal somite with row of eight spines on anterior ridge, with one transverse stria; third and fourth somites without stria.

Epistome crest without hump near mouth opening.

Eyes moderately large: maximum corneal diameter 0.3 times the distance between the bases of the anterolateral spines.

Basal segment of antennule (distal spines excluded) very long, nearly 0.5 times the carapace length, three times longer than wide (excluding spines), clearly overreaching end of corneae, with two distal spines, mesial spine shorter than lateral spine; two spines on lateral margin, proximal one short, located at midlength of segment, distal one long, not reaching end of distolateral spine (Fig. 5C). First segment of antennal peduncle with one moderately long distomesial spine nearly reaching end of second segment; second segment with two distal spines, mesial spine slightly smaller than lateral spine, exceeding third segment; third segment unarmed (Fig. 5C).

With Mxp 3 ischium about 1.5 times the length of the merus, measured along the dorsal margin, and bearing a spine distoventrally; merus with two spines on flexor margin, distal margin smaller; extensor margin unarmed (Fig. 5D).

With P1s subequal in length, about 2.5 times carapace length, squamous, with numerous non-iridescent uniramous and plumose setae, denser on mesial borders of articles. Carpus four times longer than high, as long as palm; palm slightly shorter than fingers. Merus armed with some spines, strongest spines on mesial and distal margins, reaching proximal quarter of carpus. Carpus with several spines along mesial, dorsal, and lateral sides. Palm with some spines along mesial and lateral margins, a few small spines on dorsal side. Fingers unarmed, except proximal spine on movable finger, distally curving and crossing, and ending in a sharp point (Fig. 5E).

With P2 about 2.4 times the carapace length; merus as long as the carapace, about 7.5 times as long as high, four times the carpus length and 1.6 times as long as propodus; propodus about seven times as long as high, 1.4 times dactylus length (Fig. 5F). Merus with well-developed spines along dorsal border, increasing in size distally, ventral margin with several spines and one long distal spine. Carpus with several dorsal spines, and one distoventral spine; distal margin clearly not reaching level of merocarpal articulation of P1. Propodus with six movable ventral spinules. Dactylus slightly curving distally, with eight movable spinules along entire ventral margin, last spinule very close to the end of the dactylus (Fig. 5G). P3 length 0.9 times P2 length, with similar spination and article proportions as in P2 (Fig. 5H). P4 length 0.8 times P2 length; merus nearly half the length of the P2 merus. Merus and carpus less spinose than those of P2 and P3 (Fig. 5I); merocarpal articulation ending at the level of the anterior branch of the cervical groove.

Remarks: Munida oblongata sp. nov. belongs to the group of species with five spines on the lateral margin of the carapace behind the cervical groove, eyes moderately large, the second abdominal segment with spines, the lateral parts of the posterior thoracic sternites without granules, rostrum spiniform, the epistome crest without a hump near the mouth opening, the basal article of the antennular segment very elongate, with the distomesial spine clearly shorter than the distolateral spine, the distomesial spine of the second antennal article not reaching the end of the fourth article, and with the distal half of the ventral border of the dactylus unarmed. The closest relative is *M. parca* from New Caledonia. The two species can be distinguished according to the following characters.

1. The supraocular spines reach the midlength of the rostrum in the new species, being clearly shorter in *M. parca*.
2. The basal segment of the antennular peduncle is three times longer than wide (excluding spines) in the new species, being less than 2.5 times that in *M. parca*.
3. The distal spines of the second segment of the antennal peduncle exceed the third segment in *M. oblongata* sp. nov., whereas these spines never reach the end of the third segment in *M. parca*.
4. The dorsal side of the P1 palm is armed with rows of spines in *M. parca*, whereas these spines are absent in the new species.
5. The movable spinules along the flexor margin of the dactylus of P2–P4 nearly reach the tip of the

article in the new species; this margin is unarmed in the distal third in *M. parca*. Furthermore, the dactyli are more curved in *M. parca* than in the new species.

On the other hand, *M. oblongata* sp. nov. can be easily distinguished from *M. caeli* sp. nov. and *M. lailai* sp. nov. by the following aspects.

1. The supraocular spines reach the midlength of the rostrum in *M. oblongata* sp. nov., being shorter in *M. caeli* sp. nov. and *M. lailai* sp. nov.
2. The basal segment of the antennular peduncle (excluding spines) is clearly longer in *M. oblongata* sp. nov. than in *M. caeli* sp. nov.
3. The distomesial spine of the second segment of the antennal peduncle overreaches the third segment in *M. oblongata* sp. nov., whereas in *M. lailai* sp. nov. the spine never reachs the end of the third segment, and in *M. caeli* sp. nov. the spine slightly exceeds it.
4. The dorsal side of the P1 palm is armed with rows of spines in *M. caeli* sp. nov. and *M. lailai* sp. nov., whereas these spines are absent in *M. oblongata* sp nov.
5. The movable spinules along the flexor margin of the dactylus of P2–P4 nearly reach the tip of the article in *M. oblongata* sp. nov. This margin lacks spinules in the terminal third in *M.caeli* sp. nov. and *M. lailai* sp. nov. Besides, the dactyli are more slender in *M. lailai* sp. nov. and *M. caeli* sp. nov. than in the new species.

Distribution: Solomon Islands, at a depth of between 728 and 777 m.

PARAMUNIDA LOPHIA SP. NOV. (FIG. 6)

Material examined: Solomon Islands. SALOMON 1. Stn 1831, 10°12.1′S, 161°19.2′E, 5 October 2001, 135–325 m: 1 M, 10.2 mm (holotype, MNHN-Ga6512); 2 M 13 mm (paratypes, MNHN-Ga6513). SALOMON 2. Stn 2191, 08°23.8′S, 159°27.1′E, 24 October 2004, 300 m: 1 ov. F, 10.2 mm (paratype, MNHN-Ga6514). Stn 2199, 7°43.3′S, 158°29.6′E, 25 October 2004, 296–304 m: 3 M, 9.1–11.8 m (paratypes, MNHN-Ga6515).

Etymology: From the Greek, *lophia*, for crest or ridge, referring to the longitudinal carina along the ventrolateral side of the second segment of the antennal peduncle. The name may be considered as a noun in apposition.

Description: Carapace as long as broad, excluding rostrum. Dorsal surface covered with minute spinules, with some scattered small spines and short uniramous setae. Gastric region distinctly separate from hepatic area, metagastric region well-defined; two small epigastric spines behind supraocular spines, and a median row of three well-developed spines, with the first thicker than the others. Cervical groove distinct. Cardiac region circumscribed, feebly convex, with a median row of three well-developed spines, and with the first thicker than the others. Anterior branchial region slightly separated from posterior branchial region. Frontal margin concave behind eye. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine short, reaching sinus between the rostral and the supraocular spines (Fig. 6A). Rostral spine spiniform, with thin, dorsal longitudinal carinae; supraocular spines well-developed and half as long as, and more slender than, rostrum (Fig. 6B). Lateral margins with some uniramous iridescent setae and some plumose non-iridescent setae.

Fourth thoracic sternite with few arcuate striae; fifth to seventh sternites smooth (Fig. 6C). Two median well-developed spines on anterior and posterior ridges of second and third abdominal somites. Fourth abdominal somite similar to preceding ones, but posterior ridge with distinct single median spine. Some small spiniform granules along anterior and posterior ridges of each somite.

Eye large: maximum corneal diameter about 0.3 times the distance between the bases of the external orbital spines.

Basal segments of antennule (distal spines excluded) overreaching corneae, with distomesial spine shorter than distolateral spine. First segment of antennal peduncle with anterior prolongation overreaching end of antennular peduncle, with long iridescent setae along mesial lateral margin. Second segment (spines excluded) about 1.5 times the length of the third segment, and 1.3 times longer than wide; distomesial spine long, mucronated, clearly exceeding antennal peduncle; distolateral spine not overreaching third segment. Ventral surface of second segment smooth, with a longitudinal carina along ventrolateral side; iridescent long setae along lateral side of distomesial spine continuing along ventrolateral crest. Third segment elongate, twice longer than wide and unarmed (Fig. 6D).

With Mxp 3 ischium about 1.5 times the length of the merus, measured along the dorsal margin, and bearing a spine distoventrally; merus with median, well-developed spine on flexor margin; extensor margin unarmed (Fig. 6E).

With P1 long and slender, between four and five times the carapace length, squamate, with some uniramous iridescent setae and some plumose non-iridescent setae, more dense along mesial margins. Mesial margins of merus, carpus, and palm with some small spines and acute scales. Carpus more than five

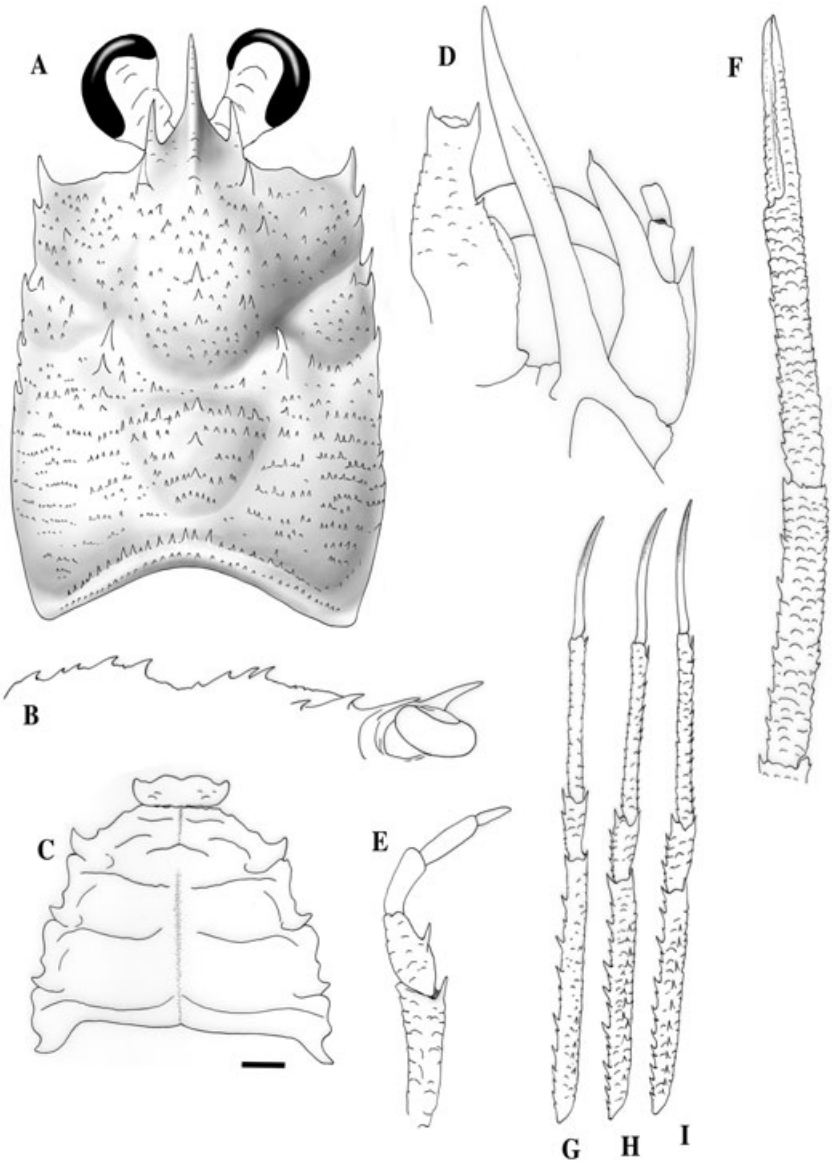

Figure 6. ***Paramunida lophia*** **sp. nov.**, male holotype, 10.2 mm (MNHN-Ga6512). Solomon Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right third maxilliped, lateral view. F, right cheliped, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, B, C = 1 mm; F, G, H, I = 2 mm ; D, E = 0.5 mm.

times longer than high. Palm as long as the carpus, and 1.4–1.5 times the length of the fingers (Fig. 6F).

With P2–P4 long and slender, subequal in length, with numerous scales on lateral sides of meri, carpi, and propodi; some uniramous iridescent setae and some plumose non-iridescent setae along dorsal and ventral borders. P2 about 3.5 times the carapace length; merus 1.5 times longer than carapace, about 10–11 times as long as high, 4.0–4.5 times as long as carpus and 1.4–1.7 times as long as propodus; propodus 9.5–10 times long as high, and 1.2–1.4 times the dactylus length (Fig. 6G). Merus with well-developed spines on dorsal border, increasing in size distally, ventral margin with a few spines, and one well-developed distal spine. Row of small spines along lateroventral margin. Carpus with some small dorsal spines; well-developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spinules. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus nearly reaching end of P1 merus. P3 with similar spination and article proportions as P2. Merus slightly shorter than P2 merus; propodus and dactylus slightly longer

than those of P2 (Fig. 6H). P4 length 0.8–0.9 times the P2 length. Merus about 1.2–1.3 times the carapace length. Propodus and dactylus subequal to those of P3 (Fig. 6I). Merocarpal articulation falling short of anterior prolongation of first segment of antennal peduncle.

Remarks: The new species is close to *Paramunida salai* sp. nov. from the Solomon Islands (see below), and to *Paramunida belone* Macpherson, 1993 from New Caledonia, Futuna, Fiji, Tonga, and the Bali Sea (Macpherson, 1993, 2004; Baba, 2005). The three species are characterized by having a rostral spine that is larger than the supraocular spines, the thoracic sternites with a few arcuate striae, and the distomesial spine on the second antennal segment mucronated and reaching, or overreaching, the end of the fourth article.

The differences among the three species are provided in the Remarks section of *P. salai* sp. nov. (see below).

Distribution: Solomon Islands, at a depth of between 135 and 325 m.

PARAMUNIDA SALAI SP. NOV. (FIG. 7)

Material examined: Solomon Islands. SALOMON 1. Stn 1831, 10°12.1′S, 161°19.2′E, 5 October 2001, 135–325 m: 93 M, 6.4–11.5 mm; 49 ov. F, 8.2–10.7 mm (holotype ov. F, 8.6 mm, MNHN-Ga6517); 21 F, 6.7–8.8 mm (paratypes, MNHNGa-6516). Stn 1834, 10°12.2′S, 161°17.8′E, 5 October 2001, 225–281 m: 2 ov. F, 8.8–9.0 mm (paratypes, MNHN-Ga6518).

Etymology: This species name is dedicated to Enric Sala, for his contributions to marine conservation biology.

Description: Carapace nearly as long as broad, excluding rostrum. Dorsal surface covered with numerous spinules. Gastric region with two epigastric spines and a median row of three spines, with the first thicker than the others. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of three well-developed spines, with the first thicker than the others. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine short, clearly not reaching the sinus between the rostral and the supraocular spines (Fig. 7A). Rostral spine spiniform, with thin dorsal longitudinal carina; supraocular spines well-developed, and half as long as, and more slender than, rostrum (Fig. 7B).

Fourth thoracic sternite with a few arcuate striae, fifth to seventh nearly smooth, with one or two striae on each side (Fig. 7C).

Second and third abdominal somites each with two well-developed median spines on anterior and posterior ridge; ridges with numerous spinules and a few small spines. Fourth abdominal somite similar to preceding ones, but posterior ridge with distinct single median spine.

Eye large: maximum corneal diameter about 0.3 times the distance between the bases of the external orbital spines.

Basal segments of antennule (distal spines excluded) exceeding corneae, with distomesial spine small, and slightly shorter than distolateral spine (Fig. 7D). Anterior prolongation of first segment of antennal peduncle clearly overreaching antennular peduncle by about 0.25 of its length. Second segment (spines excluded) about twice the length of the third segment, and twice longer than wide, ventral surface without scales, with longitudinal carinae along ventrolateral margin; distomesial spine mucronated, reaching or slightly overreaching antennal peduncle, overreaching midlength of anterior prolongation of first article, although not reaching end of basal article of antennule (excluding distal spines), distolateral spine reaching or overreaching third segment, dorsomesial margin with longitudinal carina; third segment nearly twice longer than wide, and unarmed (Fig. 7D).

With Mxp 3 ischium about 1.5 times the length of the merus, measured along the dorsal margin, and bearing a spine distoventrally; merus with median well-developed spine on flexor margin; extensor margin unarmed (Fig. 7E).

With P1 long and slender, between 4.8 and 5.9 times the carapace length; carpus slightly longer than palm, and 5.5 times longer than high; palm of chelipeds nearly as long as fingers. Mesial margins of merus, carpus and palm with small spines and acute scales (Fig. 7F).

With P2–P4 long and slender, with numerous scales on lateral sides of meri, carpi, and propodi. P2 slightly shorter than P3, and longer than P4. P2 about 3.5 times the carapace length; merus 1.5 times longer than carapace, about 10–12 times as long as high, 4.5 times as long as carpus, and 1.4–1.6 times as long as propodus; propodus about ten times as long as high, and 1.2–1.4 times the dactylus length (Fig. 7G). Merus with well-developed spines on dorsal border, increasing in size distally, ventral margin with a few spines, and one well-developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well-developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spinules. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus nearly reaching end of P1 merus. P3

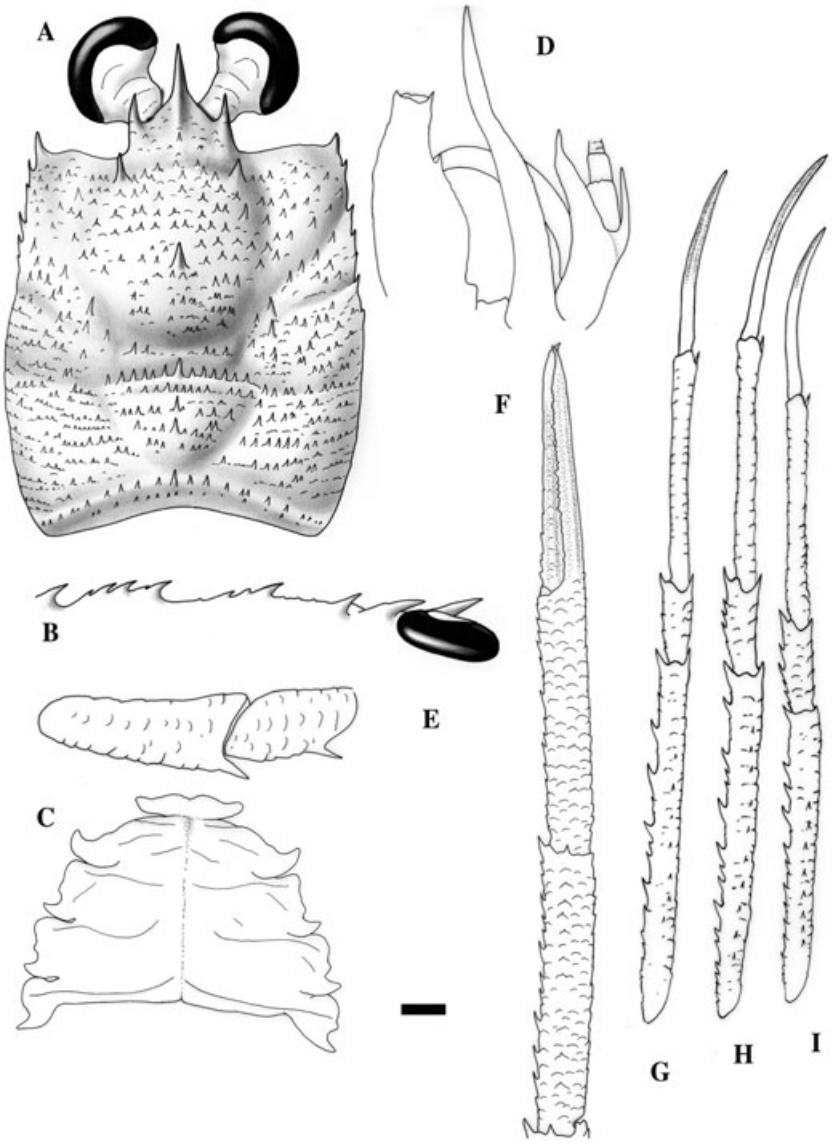

Figure 7. ***Paramunida salai*** **sp. nov.**, ovigerous female holotype, 8.6 mm (MNHN-Ga6517). Solomon Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right third maxilliped, lateral view. F, right cheliped, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, B, C = 1 mm; F, G, H, I = 2 mm; D, E = 0.5 mm.

with similar spination and article proportions as P2. Merus slightly shorter than P2 merus; propodus and dactylus slightly longer than those of P2 (Fig. 7H). P4 length 0.8–0.9 times P2 length. Merus about 1.2 times the carapace length. Propodus and dactylus slightly shorter than those of P3 (Fig. 7I). Merocarpal articulation slightly exceeding end of anterior prolongation of first segment of antennal peduncle.

Remarks: As mentioned above, *P. salai* sp. nov. is closely related to *P. belone* from New Caledonia, Futuna, Fiji, Tonga, and the Bali Sea (Macpherson, 1993, 2004; Baba, 2005), and *P. lophia* sp. nov. from the Solomon Islands. The three species can be distinguished from one another by several aspects.

Paramunida belone is easily differentiated from the two new species (*P. lophia* sp. nov. and *P. salai* sp. nov.) by the following characters.

1. The gastric region has only one median spine in *P. belone*, whereas this region has a median row of three spines, the first thicker than the others, in both *P. lophia* sp. nov. and *P. salai* sp. nov.
2. The walking legs (P2–P4) are longer in *P. belone* than in *P. lophia* sp. nov. and *P. salai* sp. nov. The

P2 merus is more than twice the carapace length in *P. belone*, and is about 1.5 times that in the two new species.

Furthermore, *P. salai* sp. nov. and *P. belone* can also be differentiated by the antennal peduncle. The distomesial spine of the second article of the antennal peduncle clearly exceeds the end of the antennal peduncle, and reaches or slightly overreaches the basal article of the antennular peduncle in *P. belone*; whereas this spine only slightly overreaches the end of the antennal peduncle, and clearly does not reach the end of the basal article of the antennular peduncle, in *P. salai* sp. nov.

The antennal peduncles are also different in *P. salai* sp. nov. and *P. lophia* sp. nov. The distomesial spine of the second segment clearly exceeds the antennal peduncle in *P. lophia* sp. nov., whereas it only reaches or slightly overreaches the antennal peduncle in *P. salai* sp. nov. Furthermore, the second segment (spines excluded) is about 1.5 times the length of the third segment, and is less than 1.5 times longer than wide in *P. lophia* sp. nov. This segment is twice the length of the third segment and twice longer than wide in *P. salai* sp. nov. Finally, the P1 palm is 1.4–1.5 times longer than the fingers in *P. lophia* sp. nov., whereas it is nearly as long as the fingers in *P. salai* sp. nov.

Distribution: Solomon Islands, at a depth of between 135 and 325 m.

PLESIONIDA CONCAVA SP. NOV. (FIG. 8)

Material examined: Solomon Islands. SALOMON 2. Stn 2260, 8°04.45′S, 156°55.87′E, 3 November 2004, 399–427 m: 4 M, 10.5–12.0 mm (holotype M, 12.0 mm; MNHN-Ga6520); 3 ov. F, 11.3–12.6 mm; 1 F, 7.7 mm (paratypes, MNHN-Ga6519).

Etymology: From the Latin *concavus*, meaning concave, referring to the concavity along the lateral side of the merus of the walking legs.

Description: Carapace as long as broad. Dorsal surface covered with numerous small spines. One epigastric spine, well-developed, behind each supraocular spine. Cardiac region slightly circumscribed. Frontal margins transverse. Rostrum 0.3 times the carapace length, compressed, slightly upturned, dorsally carinated, and not overreaching the cornea. Supraocular spines short, not reaching midlength of rostrum, and more slender than rostrum. Anterolateral spine large, reaching sinus between the rostral and the supraocular spines. Two or three small marginal spines before cervical groove. Branchial margins with four or five well- developed spines, and some small spinules. Posterior margin with numerous small spines (Fig. 8A).

Thoracic sternites smooth, without striae. Anterior part of fourth sternite narrower than third; median margin of third sternite contiguous with fourth sternite. Second to fourth abdominal somites with two transverse granulate ridges, lacking secondary transverse striae or scales; second somite without spines along anterior transverse ridge; third and fourth somites with two median spines on anterior ridge; one median spine on posterior ridge of fourth segment (Fig. 8B).

Eye large: maximum corneal diameter about 0.5 times the distance between the bases of the external orbital spines.

Basal segment of antennule (distal spines excluded) nearly reaching end of cornea, with distomesial spine shorter than distolateral spine; lateral border without spines. Anterior prolongation of first segment of antennal peduncle overreaching antennular peduncle; second segment with short distomesial spine, clearly not reaching end of third segment; third segment with small distomesial spine, clearly not reaching end of fourth segment. Second segment of antennal peduncle (spines excluded) about 1.5 times the length of the third segment, 1.5 times longer than wide; third segment as long as wide (Fig. 8C).

With Mxp 3 ischium slightly longer than the merus, and distoventrally bearing a spine. Merus with median well-developed spine on flexor margin; extensor margin unarmed (Fig. 8D).

With P1 subequal in length, between 2.5 and 3.0 times the carapace length, with a few setae; mesial margin of merus, carpus, and palm with spiniform crest, dorsal side with rows of small spines and some scattered granules. Merus shorter than carapace length, 1.5 times the length of the carpus, distomesial spine not reaching proximal fourth of carpus. Carpus 2.2–2.5 times as long as high, slightly shorter than hand. Palm slightly longer than fingers. Fingers with denticulated crest along mesial and lateral margins of movable and fixed finger, respectively, with longitudinal and rounded dorsal crest nearly reaching tips, distally curving and crossing, and ending in a sharp point; cutting edges with small teeth of various sizes (Fig. 8E).

With P2 about 2.5–2.7 times as long as carapace, with some iridescent uniramous setae, and numerous non-iridescent plumose setae, along dorsal margins of articles; merus slightly longer than carapace, about 4.5 times as long as high, nearly 3.5–4.0 times the carpus length, and 1.4–1.6 times as long as the propodus; propodus about 5.5–6.0 times as long as high, and 1.3–1.7 times longer than dactylus (Fig. 8F). Dorsal border of merus with row of spines, increasing

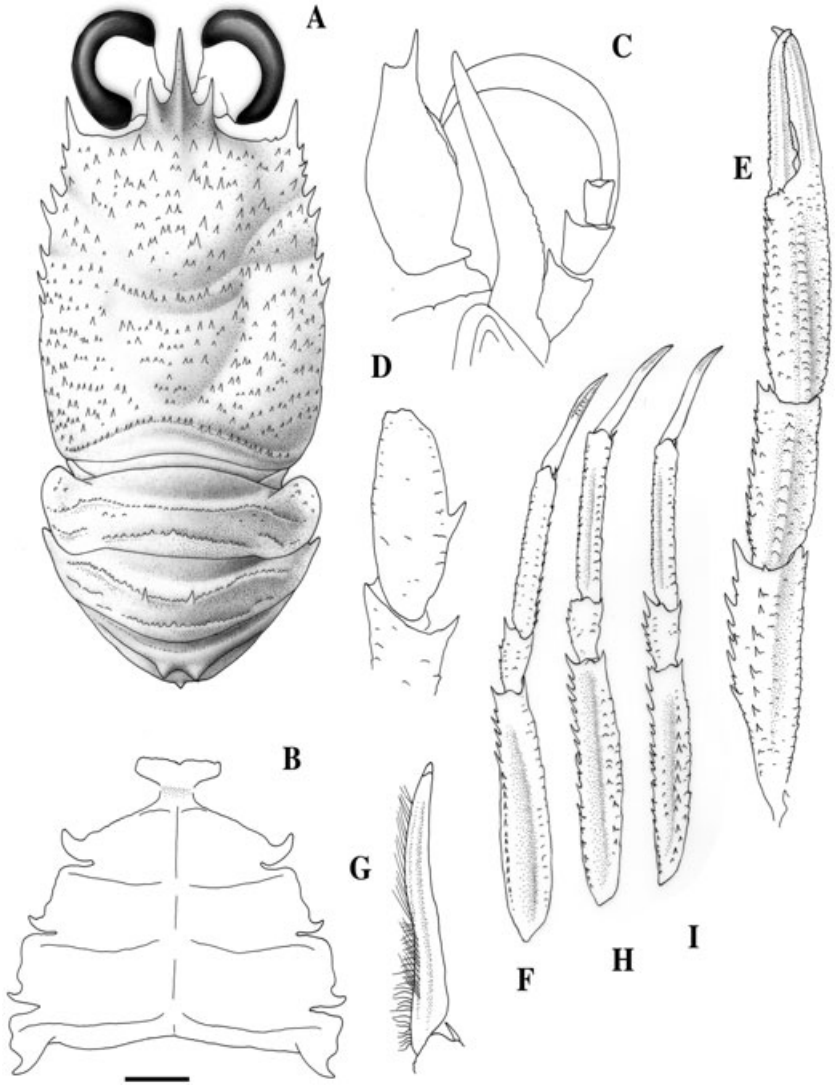

Figure 8. ***Plesionida concava*** **sp. nov.**, male holotype, 12.0 mm (MNHN-Ga6520). Solomon Islands. A, carapace and abdomen, dorsal view. B, sternum. C, left antennule and antenna, ventral view. D, ischium, and merus of right third maxilliped, lateral view. E, right cheliped, lateral view. F, right P2, lateral view. G, dactylus, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: A, E, F, H, I = 2 mm; B, C, D, G = 1 mm.

in size distally, lateral side strongly concave; ventral border with row of short spines and well-developed distal spine. Carpus with some dorsal and ventral spines, increasing in size distally; distal margin slightly overreaching merocarpal articulation of P1. Propodus with 11–12 movable spinules along ventral margin, dorsal border serrated. Dactylus slightly curving, unarmed, dorsal border proximally slightly concave (Fig. 8G). P3 length slightly shorter than P2, with similar spination and proportions among articles (Fig. 8H). P4 length 0.9 times P2; merus 0.8–0.9 times the length of the P2 merus, lateral side less concave than in previous legs; ventral spines stronger than those of P2 and P3 meri (Fig. 8I). Merocarpal articulation ending at distal margin of corneae.

Remarks: The genus *Plesionida* Baba & de Saint Laurent, 1996, at present, contains two species: *Plesionida psila* Baba & de Saint Laurent, 1996, from the New Caledonia, and Wallis and Futuna islands (Baba, 2005; Macpherson & Baba, 2006), and *Plesionida aliena* (Macpherson, 1996), from New Caledonia, Fiji and Tonga (Baba, 2005). *Plesionida concava* sp. nov. is similar to *P. aliena* (Macpherson, 1996). However, they differ in the following features.

1. The carapace is covered by numerous small spines in the new species, whereas these spines are nearly absent in *P. aliena*, with only two epigastric spines and some granules, which are more numer-

ous and acute on the hepatic and branchial regions.
2. The P1s are more spiny in the new species than in *P. aliena*. In the new species, the mesial margin of the merus, carpus, and palm has a spiniform crest, and some spines scattered on the dorsal side of the articles. In *P. aliena*, the dorsal side of the articles is unarmed, and the mesial margin of the merus, carpus, and palm is serrated.
3. The lateral side of the merus of P2–P4 is concave in the new species and convex in *P. aliena*.

Distribution: Solomon Islands, at a depth of between 399 and 427 m.

Molecular analysis

Genus *Agononida*

After alignment with other sequences determined for the genus *Agononida* in a previous study (Machordom & Macpherson, 2004), 1187 bp were finally examined. The 16S rRNA sequence showed a high variability region between positions 245 and 272, which required the insertion of gaps. The partial COI sequence data set obtained consisted of 657 characters, of which 428 were constant, 29 were parsimony uninformative, and 200 were parsimony informative. For the 16S rRNA gene sequence, the resulting data set comprised 530 characters, of which 381 were constant, 22 were parsimony uninformative, and 127 were parsimony informative. Saturation tests indicated no saturation when we plotted all the substitutions together, but revealed saturation for transitions in the third codon positions of the COI gene for divergence values above 15%.

Intrageneric divergences between the new species and known species of the genus *Agononida* were in the range of 3.40–13.10% for 16S rRNA, and 8.70–17.88% for the COI gene. The new species showed the least divergence from *A. similis*: 3.40% for the 16S rRNA and 8.70% for the COI. The incongruence length difference (ILD) test revealed no significant incongruence among gene partitions ($P = 0.45$), and there were no strongly supported conflicting nodes among the tree topologies, so both genes were analysed in a combined data set, and only these results are presented.

The model that fitted the combined data set best was the GTR + I + Γ model (general time-reversible model; Lavane *et al.*, 1984; Rodríguez *et al.*, 1990), which gave an α-parameter of 1.3220 and an I-value of 0.5680. Base frequencies were A = 0.3220, C = 0.1480, G = 0.1739, and T = 0.3560, and the proportions of changes were 1.5688, 7.3481, 2.8003, 0.2082, and 16.2166. The selected outgroup was *Crosnierita dicata* (Macpherson, 1998), which was the closest genus to *Agononida* (Machordom & Macpherson, 2004). The species *Alainius crosnieri* Baba, 1991 was also included to test for a non-monophyletic origin of the genus. Relationships at terminal nodes were highly supported by bootstrap and posterior probability values (Fig. 9). At deep nodes, relationships were unresolved, and there was no support for the monophyly of the genus *Agononida*, but the new species in this genus was highly supported. Relationships among the different species exhibited a first cluster including *A. isabelensis* sp. nov. + *A. similis*, which was highly supported in all of the analyses. The sister group of this cluster was *Agononida procera* Ahyong and Poore, 2004, which was supported by all of the analyses. The species *Agononida marini* (Macpherson, 1994) appeared as a sister group of these three species, although support for this position was very low. The phylogenetic positions of the species *Agononida sphecia* (Macpherson, 1994) and *Agononida incerta* (Henderson, 1888) were not resolved.

Genera *Paramunida* and *Plesionida*

After alignment with other sequences of the genera *Paramunida* and *Plesionida*, determined in a previous study (Machordom & Macpherson, 2004), 1197 bp were finally analysed. The 16S rRNA sequence showed a high variability region between positions 245 and 272, requiring the insertion of gaps.

The partial COI sequence data set obtained for the two new species of the genus *Paramunida*, and for the new species of *Plesionida*, consisted of 657 characters, of which 437 were constant, 24 were parsimony uninformative, and 196 were parsimony informative. For the 16S rRNA gene sequence, the resulting data set comprised 540 characters, of which 398 were constant, 36 were parsimony uninformative, and 106 were parsimony informative. Saturation tests revealed no saturation for 16S rRNA and COI when we plotted all substitutions together. Intrageneric divergences within the *Paramunida* genus were in the range of 1.54–12.05% for the gene 16S rRNA, and of 2.95–17.35% for the COI. The lowest divergences for 16S rRNA were observed between *P. salai* sp. nov. and *P. belone*, and the lowest values for the COI sequences were detected between *P. salai* sp. nov. and *P. lophia* sp. nov.

For the genus *Plesionida*, the divergence between *P. aliena* and *P. concava* sp. nov. was 5.7% for 16S rRNA, and 10.85% for COI. The ILD test indicated no significant incongruence among gene partitions ($P = 0.48$), and there were no strong incongruences between the tree topologies, so both genes were analysed in a single matrix, and only the results of the combined data set are provided here.

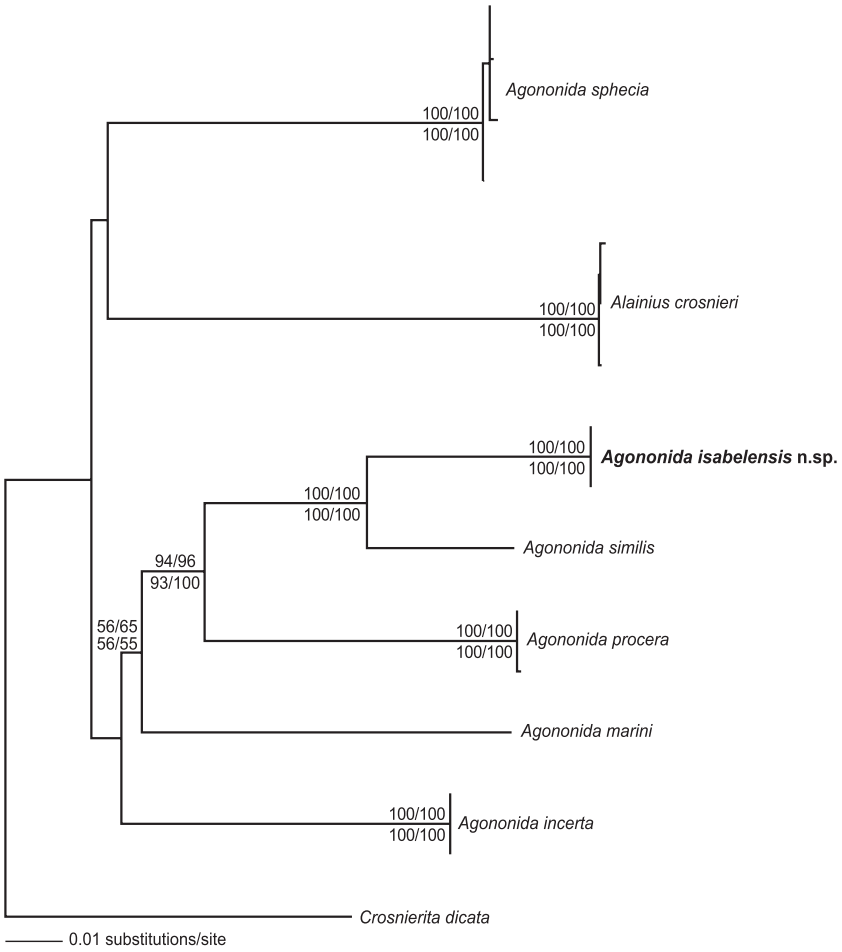

Figure 9. Neighbour-joining (NJ) tree based on the combined data set (16S rRNA and COI genes) showing phylogenetic relationships among *Agononida*. Numbers above branches indicate bootstrap values for the NJ and maximum parsimony (MP) analyses. Numbers below branches indicate bootstrap values for the maximum likelihood (ML) analyses and Bayesian posterior probabilities (BPPs).

The model that best fitted this combined data set was the GTR + I + Γ model (Lavane *et al.*, 1984; Rodríguez *et al.*, 1990), which gave an α-parameter of 1.4558 and an I-value of 0.6286. Base frequencies were A = 0.3234, C = 0.1371, G = 0.1664, and T = 0.3730, and the proportions of changes were 1.1171, 7.5925, 3.5999, 0.00001, and 17.8696.

The species *Onconida alaini* Baba & de Saint-Laurent, 1996 was selected as the outgroup, on the basis of previous results (Machordom & Macpherson, 2004) that showed the genus *Onconida* as the closest related genus to *Paramunida* and *Plesionida*. The monophyly of the genus *Paramunida* was highly supported by all of the tests (Fig. 10), although not all relationships within the genus were fully resolved. The phylogenetic relationship between the two new species *P. salai* sp. nov. and *P. lophia* sp. nov. was highly supported as a sister group, and these two species were in turn the sister group of the species *P. belone*.

The relationship between the species *Paramunida stichas* Macpherson, 1993 and *Paramunida proxima* (Henderson, 1885) was supported by all of the analyses. A comparison between samples of *P. stichas* from the Solomon Islands and from New Caledonia revealed two different groups separated by a mean divergence of around 1.1% for both genes (Fig. 10).

The last supported cluster included all of the species of the genus, except the species *Paramunida granulata* (Henderson, 1885), which always occupied a basal position. Relationships among the remaining species were not resolved.

Our analysis of two of the three species described for the genus *Plesionida* supported the monophyly of the group, with *P. aliena* as the sister group of *P. concava* sp. nov.

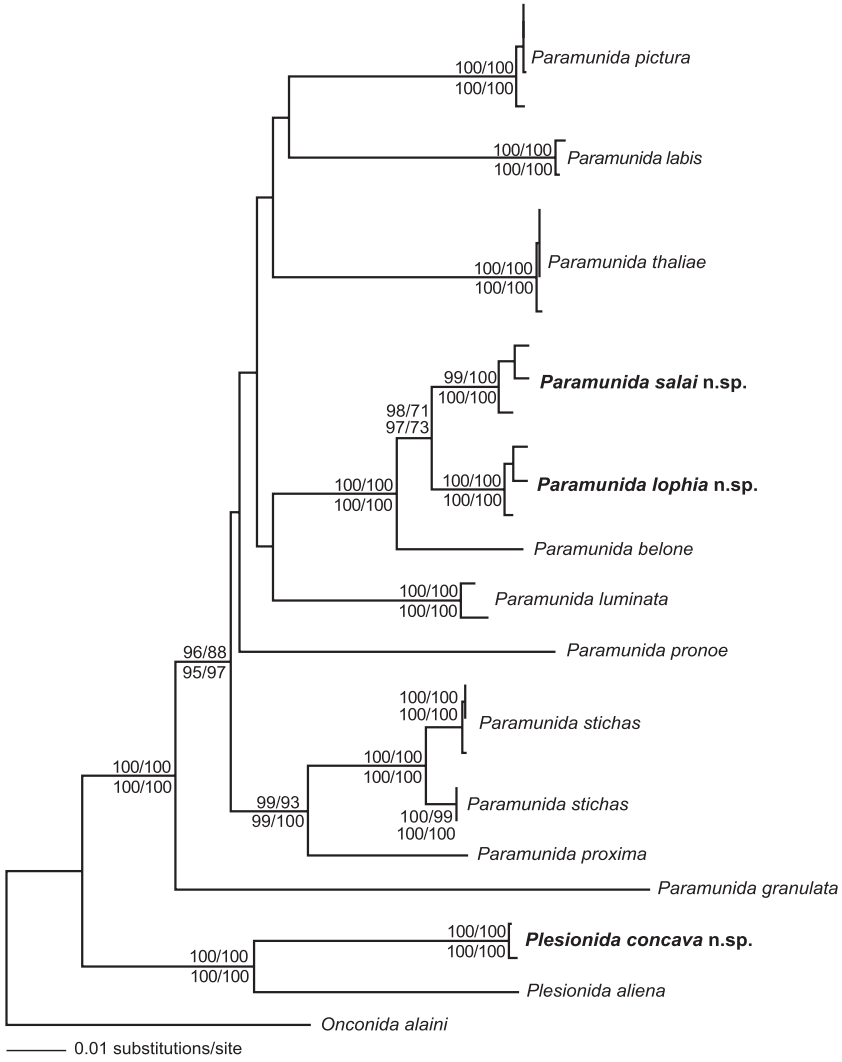

Figure 10. Neighbour-joining (NJ) tree based on the combined data set (16S rRNA and COI genes), showing phylogenetic relationships between *Paramunida* and *Plesionida*. Numbers above branches indicate bootstrap values for the NJ and maximum parsimony (MP) analyses. Numbers below branches indicate bootstrap values for the maximum likelihood (ML) analyses and Bayesian posterior probabilities (BPPs).

GENUS *MUNIDA*

After alignment with other sequences of the genus *Munida* determined in a previous study (Machordom & Macpherson, 2004; Macpherson & Machordom, 2005), 1199 bp were finally analysed. As for the other genera, the 16S rRNA gene showed a high variability region between positions 245 and 272 that required the insertion of gaps. The partial COI sequence data set obtained for the genus *Munida* consisted of 657 characters, of which 392 were constant, 19 were parsimony uninformative, and 246 were parsimony informative. For the 16S rRNA gene sequence, the resulting data set comprised 542 characters, of which 327 were constant, 50 were parsimony uninformative, and 165 were parsimony informative. Intrageneric divergence for the genus was in the range of 0.69–13.26% for the 16S rRNA gene, and of 3.50–20.24% for COI. The ILD test revealed no significant incongruence among the gene partitions ($P = 0.96$), and as for the other genera there were no incongruent topologies, so both genes were analysed in a single matrix. We also analyzed the 16S rRNA gene separately, as the COI gene could not be amplified in some species.

Tests for the 16S rRNA gene rendered no signs of saturation, but the COI gene sequence exhibited a certain level of saturation in transitions when all substitutions were plotted together, and also for third codon positions.

The model that best fitted the combined data set was the K81uf + I + Γ model (Kimura 3-parameters

model; Kimura, 1980), which gave an α-parameter of 0.5357 and an I-value of 0.5253. Base frequencies were A = 0.3893, C = 0.1068, G = 0.0969, and T = 0.4070, and the proportions of changes were 1.0000, 19.4012, 1.5268, 1.5268, and 19.4012. Model HKY + I + Γ (Hasegawa, Kishino & Yano, 1985) was selected for the ML analyses.

The model that best fitted the 16S rRNA data set was the TVM + I + Γ model (transversional model), which gave an α-parameter of 0.6255 and an I-value of 0.4306. Base frequencies were A = 0.3988, C = 0.0698, G = 0.1364, and T = 0.3950, and the proportions of changes were 1.2190, 19.2918, 2.6905, 0.0000, and 19.2918. Model GTR + I + Γ (Lavane *et al.*, 1984; Rodríguez *et al.*, 1990) was selected for the ML analyses.

The relationships of the genus *Munida* with other genera of the family remain unclear, therefore the species *Eumunida sternomaculata* de Saint Laurent and Macpherson, 1990 was selected as the outgroup, on the basis of previous studies (Morrison *et al.*, 2002; Machordom & Macpherson, 2004). Analysis of the combined data set (data not shown), and the 16S rRNA data set separately (Fig. 11), indicated two main clusters.

In the combined data set the basal cluster included the species *Munida delicata* Macpherson, 2004, and the type species of the genus *Munida rugosa* (Fabricius, 1775) from the North-East Atlantic, and the second cluster included the rest of the species of the genus. The basal group was supported in all of the analyses, with higher support in the Bayesian analyses than that indicated by the bootstrap. Divergences between these two species were quite high: 8.69% for the 16S rRNA gene and 15.80% for the COI gene. The second cluster was well supported except by the results of the Bayesian analysis.

As the COI gene sequence could not be amplified in the new species *M. oblongata* sp. nov., as in the species *Munida devestiva* Macpherson, 2006, the 16S rRNA gene sequence was analysed separately. In this analysis, these two species appeared in a basal cluster together with the species *M. rugosa* and *M. delicata* (Fig. 11). The type species *M. rugosa* was the sister lineage of the other three species, although bootstrap values and posterior probabilities were low. Divergence was in the range of 8.69–13.06%, which is high compared with that shown by the remaining species of the genus. The second cluster was divided into two different subgroups. All of the newly described species were included in the first subgroup. The species *M. lailai* sp. nov. appeared as the sister group of the species *M. parca* with high support. Divergence between these two species was low: 0.69% for the 16S rRNA gene and 4.75% for the COI gene. The species *M. caeli* sp. nov. was the sister lineage of these two species, also with high support, showing mean divergences of 1.87% (16S rRNA) and 7.45% (COI) from *M. parca*, and 1.64% and 8.11% from *M. lailai* sp. nov., respectively. The phylogenetic relationship of the species *M. mendagnai* sp. nov. was not fully resolved, although in all tree topologies it occupied a basal position in the first subgroup.

DISCUSSION

We described here eight new species of the family Galatheidae from the South-West Pacific, based on morphological and molecular data. We used molecular data to elucidate the phylogenetic relationships of the new species at the genus level.

Agononida

None of our analyses recovered the monophyly of the genus, in line with the results of a previous study (Machordom & Macpherson, 2004). In the present paper, we only inferred phylogenetic relationships among the newly described species and another five species of the genus. This results from the complexity of developing molecular analyses for the group, as we failed to amplify the COI gene for several species, making it difficult to establish relationships with a high level of confidence.

Despite this problem, our analyses were able to recover, with high support, the relationship between the new species, *A. isabelensis* sp. nov., and its sister group, *A. similis*, which is morphologically very similar. The two species can be easily differentiated according to the number of spines along the branchial margin of the carapace, and the number and size of spines on the basal article of the antennular peduncle, confirming the phylogenetic value of these characters. The relationship between this cluster and the species *A. procera* was also highly supported. The species *Alainius crosnieri* was also included in the analyses to check for the possibility of a polyphyletic origin of the group. Although all of the tree topologies located this species within the ingroup, this was not highly supported in any of the analyses. Further work is still required to clarify the apomorphic characters of the group, and its origin and diversification.

Paramunida and *Plesionida*

The genus *Paramunida* was identified with high support as a monophyletic group in all of the analyses, confirming the results of previous studies based on morphological and molecular characters (Baba, 1988; Machordom & Macpherson, 2004). The two new species described, *P. lophia* sp. nov. and *P. salai* sp. nov., were recovered as sister lineages, and showed

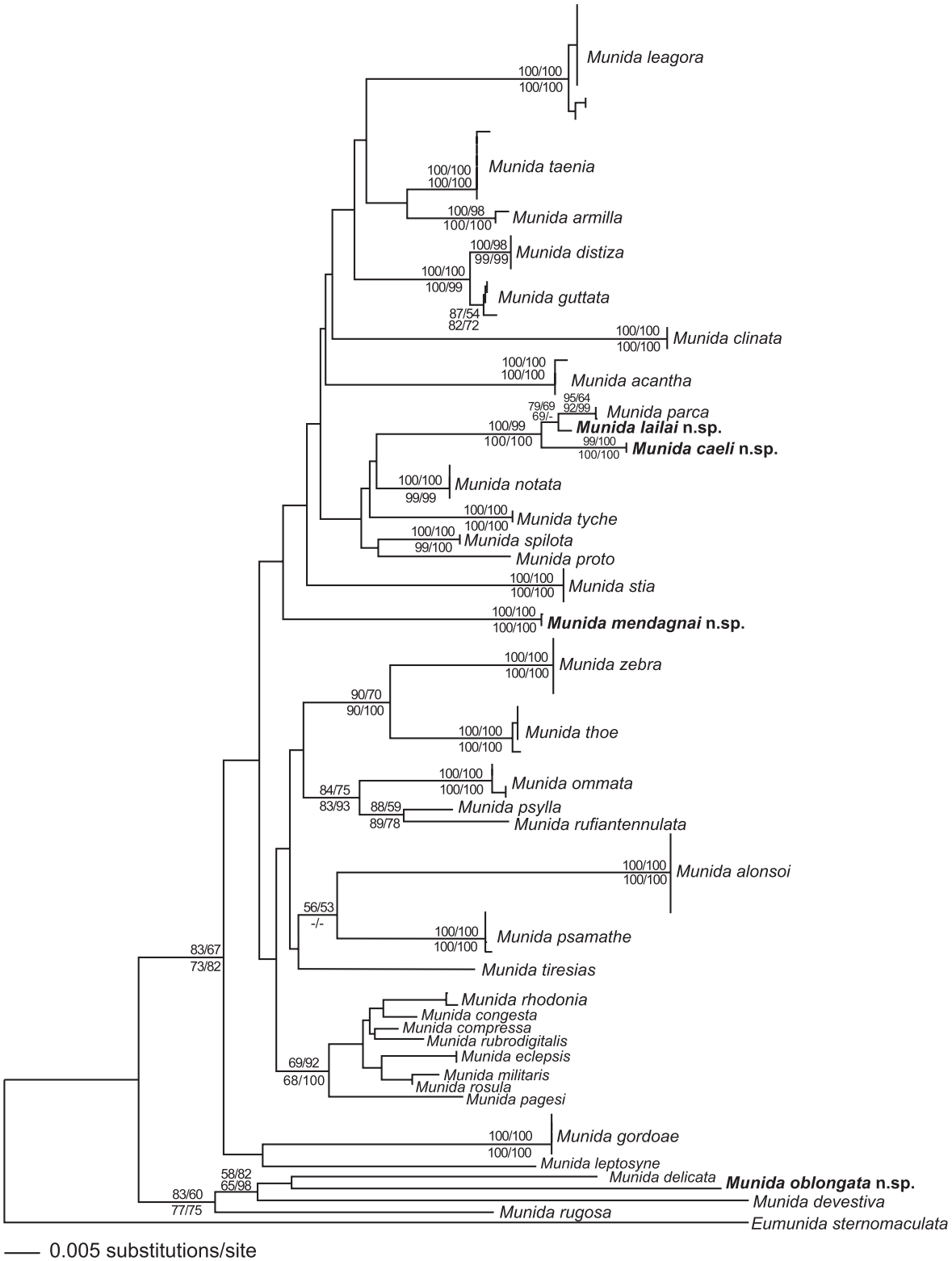

Figure 11. Neighbour-joining (NJ) tree based on the 16S rRNA data set showing phylogenetic relationships among *Munida*. Numbers above branches indicate bootstrap values for the NJ and maximum parsimony (MP) analyses. Numbers below branches indicate bootstrap values for the maximum likelihood (ML) analyses and Bayesian posterior probabilities (BPPs).

the lowest interspecific average divergence reported for the genus (1.9% for the 16S rRNA gene and 3.1% for the COI gene). Our morphological data support the taxonomic status of these two species, and diagnostic characters were constant in all specimens analysed. *Paramunida belone* appeared with high support as the sister group of the two new species, and also showed scarce divergence with respect to both species.

Low divergences seem to be a common pattern within this genus, with the exception of the species *P. granulata*. This last species is characterized by having a very long distomesial spine in the second article of the antennal peduncle, which is clearly shorter in the other species of the genus (Baba, 1988). This morphological difference, along with spinulation of the dorsal surface of the carapace, supports the divergence of *P. granulata* from the other species. In contrast, morphological differences between the two new species and *P. belone* were based on the shape of the antennal peduncle, suggesting that this appendix, as in *P. granulata*, is of phylogenetic value in the genus.

Specimens of the species *P. stichas* from the Solomon Islands were compared with others collected in the region of New Caledonia. These analyses differentiated the two areas, indicating a high mean intraspecific divergence of around 1.1% for both genes. The study of the mitochondrial gene ND1 (not included in this study) revealed the same tree topology, with a lower divergence value than the divergence indicated by the two genes analysed here (P. Cabezas, A. Machordom, E. Macpherson., unpubl. data).

Such low divergence values might be explained by a recent speciation event, or by speciation accompanied by slow morphological and molecular changes. This last scenario suggests a slow DNA substitution rate for this complex of species, a phenomenon that has been previously reported in other crabs and lobsters (Schubart *et al.*, 2001; Groeneveld *et al.*, 2007). A phylogeographic study of the genus in the Indo-West Pacific that is already underway, including morphological and molecular information, will help clarify the taxonomic position of *P. stichas* in the two regions, and the evolutionary history of the genus (P. Cabezas, A. Machordom, E. Macpherson., unpubl. data).

The genus *Plesionida* was analysed together with the genus *Paramunida* because only two of the three species described for the genus could be examined, and because previous studies (Machordom & Macpherson, 2004) have revealed that the genera are closely related. Our molecular analysis confirmed the taxonomic status of the genus, which had been inferred on the basis of morphological characters (Macpherson, 2004). *Plesionida concava* sp. nov. was compared with *P. aliena*, which is distributed in New Caledonia, Fiji, and Tonga. These two species were resolved with high support as a monophyletic group. A future analysis of the third species described for the genus will complete our knowledge of this group.

Munida

The genus *Munida* is by far the most diverse taxon of the family Galatheidae, and is widely represented in the waters of the South-West Pacific. In an earlier study, we suggested the monophyly of the group in the area (Machordom & Macpherson, 2004), excluding the species *Munida callista* Macpherson, 1994, which was recently ascribed to a new genus (Cabezas *et al.*, 2008). The complexity of the group has previously been described in terms of extreme morphological convergence and heterogeneity in divergence values within species (Baba, 2005; Macpherson & Machordom, 2005).

The study of the combined data set and the separate 16S rRNA data set supported two differentiated clusters. The first cluster occupied a basal position, and included the type species *M. rugosa* from the North-East Atlantic and *M. delicata* from the Solomon Islands, whereas the species *M. oblongata* sp. nov. from the Solomon Islands and *M. devestiva* from New Caledonia were also included when we only considered the 16S rRNA data. Mean divergence values among the species were quite high (10.96% for 16S rRNA and 15.8% for the COI gene), but were within the range cited for other decapod taxa (Ptacek *et al.*, 2001; Harrison, 2004). For the COI gene, the value could be an underestimate because of saturation traces found in the third codon positions. For both genes, these values were higher than the mean divergence reported for the genus (Machordom & Macpherson, 2004), and similar divergence values have been found in species such as *Enriquea leviantennata* (Baba, 1988) and *Babamunida callista* (Macpherson, 1994), which were excluded from the genus *Munida* on the basis of morphological and molecular information.

Additionally, the new species *M. oblongata* sp. nov. is morphologically very close to the species *M. parca* from New Caledonia, although genetically they show a deep divergence. Although this pattern seems to be common in decapods (Knowlton, 1986), additional explanations are also possible. The undersampling of more closely related taxa might lead to the same pattern. A future increase of the sampling effort is essential to evaluate the overall diversity of galatheids in the area. And extinction events in the group could be an alternative explanation, although with our data it is not possible to confirm this hypothesis.

The second cluster included the rest of the species of the genus, all from the South-West Pacific. Three new species of the genus *Munida* appeared in this cluster. Although most relationships at the internal nodes were unresolved, *M. lailai* sp. nov. was highly supported as a sister group of the species *M. parca*, and these two species were supported as a sister lineage to *M. caeli* sp. nov. Divergence values between these two species were very low, although they were similar to divergences reported for other species complexes such as *Munida militaris* Henderson, 1885 + *Munida rosula* Macpherson, 1994 + *Munida compressa* Baba, 1988 (Machordom & Macpherson, 2004). Morphologically, the two new species resemble *M. parca*, and although morphological differences are subtle, these were constant in all of the specimens examined. The phylogenetic position of the species *M. mendagnai* sp. nov. was not resolved, but it appeared in the second cluster with *M. caeli* sp. nov. and *M. lailai* sp. nov. in all the analyses. All three new species included in this cluster showed a low genetic divergence, with a very similar morphology.

This marked difference between the first and the second cluster was emphasized in a previous study (Cabezas *et al.*, 2008), in which *M. rugosa* was not included in the ingroup of the genus *Munida*, and showed a clear genetic difference with respect to the rest of species of the genus. Morphologically, there are no apparent characters to differentiate species from both clusters, although differences in epistome shape and armature, as have been observed between *Munida* and *Babamunida* (Cabezas *et al.*, 2008), as well as antenna and antennula insertions, should be considered. On the other hand, the heterogeneity observed in the divergence values could indicate that different radiation events have shaped the diversification of the genus.

All of this information emphasizes the need for further more detailed analyses of more species from the Indo-Pacific and Atlantic-Mediterranean oceans, as well as the study of more conserved genes, to clarify the taxonomy of this group of species.

Evolutionary considerations

The taxonomic status of the new species was supported by both morphological and molecular data, although intrageneric relationships could not be deduced with confidence for all of the species. This low resolution seems to be the general pattern for the family Galatheidae, and has already been noted in other studies in which relationships at the genus level were also unresolved (Machordom & Macpherson, 2004). This conspicuous feature might be related to a scenario resulting from a rapid speciation process, rather than from a lack of resolution or paucity of the molecular markers used. The number of informative positions and the low levels of saturation indicate that both genes are appropriate for the study of this group. In addition, previous works have described the mitochondrial genes 16S rRNA and COI as powerful tools to elucidate phylogenetic relationships in crustacean decapods (Porter, Pérez-Losada & Crandall, 2005), and in other marine groups (e.g. sponges; Blanquer & Uriz, 2007). Our phylogenies displayed a large number of short internal branches relative to long terminal branches. However, some groups of species also showed short terminal branches, which suggest recent speciation events.

Although the data did not show a clear geographic structure, New Caledonia seems to be the ancestral area for the different genera, although a deeper phylogeographic study is necessary to test this fact.

These results suggest an evolutionary history shaped by rapid diversification and radiation events, probably related to the marine and geological complexity of the area (Holloway & Hall, 1998).

Events of rapid diversification are common within Crustacea, including decapods (Schram, Feldmann & Copeland, 1978), making it difficult to resolve relationships at ancient nodes, and to thus estimate divergence times. The Eocene (Schram, 1986) has been proposed as the scene for extensive decapod radiation, and Machordom & Macpherson (2004) located the diversification of the genus *Munida* in the Late Miocene, using two mitochondrial genes. An older estimation has been suggested by Porter *et al.* (2005), dating the diversification of Anomuran crabs (including the Galatheidae family) in the Permian–Triassic, using a multi-locus estimation procedure based on nuclear and mitochondrial genes. It is clear that the use of mitochondrial markers alone is insufficient for resolving such ancient speciation processes, as the substitution rate leads to a high probability of homoplasy. Thus, further investigations, including additional morphological and molecular characters, are still required to understand the evolutionary history of the group.

Previous studies have demonstrated the usefulness of nuclear genes to resolve phylogenetic relationships at high taxonomic levels (Tudge & Cunningham, 2002; Ahyong *et al.*, 2007). Morphologically, the extreme convergence observed in this family makes it very difficult to find new morphological characters of phylogenetic value, and the most common morphological characters used in the traditional taxonomy of the family show a high degree of homoplasy. Nevertheless, characters not previously considered, such as those describing the epistome region, can provide new synapomorphies (Cabezas *et al.*, 2008). If combined with additional genes with lower substitution rates,

such as conserved genes, these characters could improve the resolution obtained at the basal nodes of the phylogenies.

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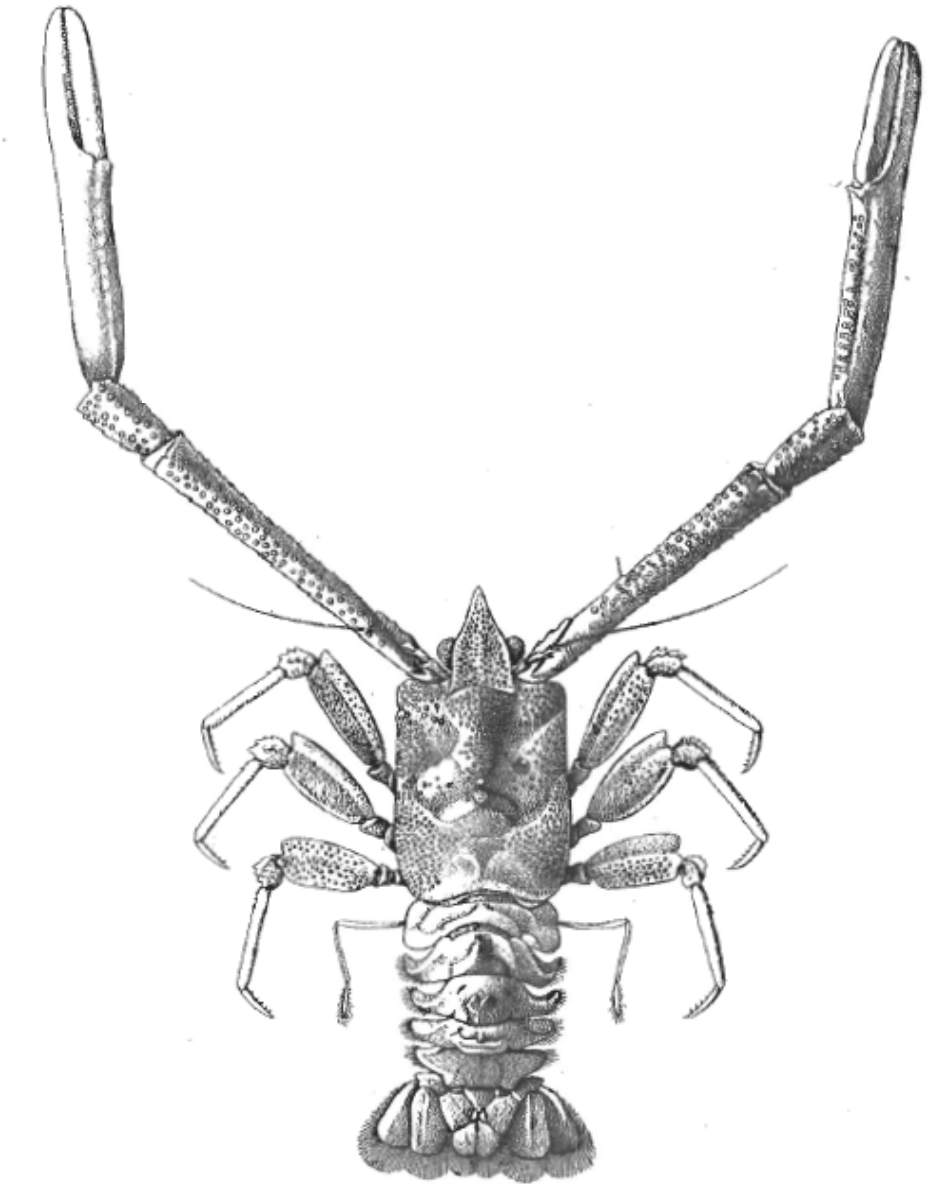

Munidopsis carinipes Faxon, 1893

CAPÍTULO III

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Allogalathea (Decapoda: Galatheidae): a monospecific genus of squat lobsters?

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Allogalathea (Decapoda: Galatheidae): a monospecific genus of squat lobsters?

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Abstract

The genus *Allogalathea* was established by Baba in 1969 to include the well-known species *Galathea elegans*. This species is widely distributed across the Indo-West Pacific Ocean and is characterized by living in close association with crinoids and by its conspicuous coloration. Although the genus is considered monospecific, different colour patterns and discrete morphological variations mainly associated with the rostrum and chelipeds have been reported. These differences could point to cryptic species questioning the monotypy of the genus. To address this issue, we sequenced the mitochondrial COI (658 bp) and 16S rRNA (882 bp) genes and the nuclear gene PEPCK (598 bp) in numerous specimens from eight different localities and also examined their morphological characters. DNA sequences were analyzed using maximum parsimony, maximum likelihood, and Bayesian approaches of phylogenetic inference. The resulting trees were combined with morphological evidence to test species boundaries. Our molecular data revealed four deeply divergent clades, which can be distinguished by subtle morphological differences in the spinulation and length-breadth ratio of the P1 carpus, spinulation of the walking legs and shape of the rostrum. Our findings indicated that *Allogalathea elegans* is in fact a species complex comprising four different species, which, although genetically very distinct, are morphologically very similar. We provide morphological descriptions and a key to these four species of the genus.

Additional keywords: Morphological characters - mitochondrial genes - PEPCK gene - molecular systematics.

Introduction

Studies on monospecific or cosmopolitan species of a wide range of both marine and terrestrial taxa have revealed that the real diversity of many groups is currently underestimated. In effect, many such taxa have been discovered to be species-complexes with a high morphological similarity but genetically distinct (Hebert *et al.*, 2004; Vovlas *et al.*, 2008; Demes, Graham & Suskiewicz, 2009).

Species identification among the squat lobsters of the family Galatheidae is proving particularly difficult due to their many conservative morphological traits (Jones & Macpherson, 2007; Cabezas, Macpherson & Machordom, 2009). Traditionally, the taxonomy of this group has been based on morphological characters but current molecular techniques have proven to be powerful tools for species delineation (Macpherson & Machordom, 2001). Within this decapod family, 12 genera are considered monospecific (e.g. *Anomoemunida* Baba, 1993, *Enriquea* Baba, 2005, *Setanida* Macpherson, 2006, *Tasmanida* Ahyong, 2007). However, there are few records of any of these monospecific taxa and there is also limited collected material with the exception of the genus *Allogalathea*, for which numerous records and specimens are available.

The genus *Allogalathea* was established in 1969 by Baba to include the well-known species *Galathea elegans* Adams & White, 1848, whose original description was based upon specimens collected in Corregidor, the Philippines. Nevertheless, a number of taxa are now considered junior synonyms of *A. elegans*: *Galathea longirostris* Dana, 1852, from the Fiji Islands found at 18 m; *G. grandirostris* Stimpson, 1858, from Kagoshima Bay, Japan at 9 m; *G. deflexifrons* Haswell, 1882, from Albany Passage, Queensland; and *G. longirostris* Yokoya, 1936, from Misaki, Sagami Bay, Japan. A complete list of citations and synonymies of *A. elegans* is provided in Baba *et al.* (2008, 2009). Unfortunately, the type specimens of *G. longirostris* Dana, 1852, *G. longirostris* Yokoya, 1936, and *G. grandirostris* Stimpson, 1858 are lost. The type specimen of *G. deflexifrons* Haswell, 1882 at the Australian Museum is preserved dry and its morphological details are obscure (e.g. an epipods study) making a careful examination of the specimen without damaging difficult.

Allogalathea elegans is considered a shallow water species living at depths between 0 to 146 m, usually associated with crinoids and widely

distributed in the Indo-West Pacific region. The species has been cited from the eastern coast of Africa to the Fiji Islands and from Japan to southern Australia (Baba *et al.*, 2008, 2009). This genus is easily differentiated from other genera of the family Galatheidae by a triangular rostrum, which is extremely elongate, dorsally flattened and ventrally carinate, with 5-9 lateral teeth, and by a carapace with setiferous striae (Baba, 1969). Previous works have reported different colour patterns in this species (Miyake, 1938; Baba, 1979) and the study of numerous specimens from Indonesia revealed small differences in the setation and spinulation of the chelipeds (Baba, 1979). Further, the presence and number of epipods on the pereiopods and the relative length of the rostrum also vary. This variability suggests that the occurrences of *A. elegans* mentioned by different authors should be revised in order to evaluate the morphological differences previously reported and the relative importance of the different colour patterns.

A large number of specimens of *Allogalathea* have been collected in numerous expeditions over the past decades in the Indian and western Pacific Oceans. Here, we re-examine all this material in addition to the type material of *A. elegans* from Corregidor (the Philippines), using a combined morphological and molecular approach based on two mitochondrial (cytochrome oxidase I, COI and 16S rRNA) and one nuclear marker (phosphoenolpyruvate carboxykinase, PEPCK). Mitochondrial genes have been typically used to elucidate phylogenetic relationships in the family Galatheidae (Lin, Chan & Chu, 2004; Cubelio *et al.*, 2007; Schnabel, Martin & Moffitt, 2009). We also selected the PEPCK marker for this study since this nuclear gene has shown good potential for resolving relationships in decapods at high taxonomic levels (Tsang *et al.*, 2008; Ma, Chan & Chu, 2009) and the high divergence values reported by Tsang *et al.* (2008) for three species of *Panulirus* (approximately 6%) suggested it is also capable of resolving species-level relationships.

Our results revealed the existence of four different species that are genetically distinct yet morphologically very similar. Previous records of *Allogalathea* species are provisionally revised when a description and illustrations are available. However, the existence of additional species of *Allogalathea* is likely and a more detailed study including more specimens from other regions in combination with molecular data would be desirable.

Material and methods

Sampling and identification

Specimens were collected by divers or using beam trawls or Waren dredges in numerous expeditions to the western Pacific, e.g. Taiwan, Mariana Islands, Philippines, Indonesia, Vanuatu, New Caledonia, and western Indian ocean, e.g. Madagascar, Mozambique channel, Red Sea. The measurements of specimens provided are postorbital carapace lengths. The terminology used mainly follows that of Zariquiey-Alvárez (1952), Baba and de Saint Laurent (1996) and Baba (2005). Following Baba (2005), the terms flexor and extensor borders of articles are only used for the maxilipeds and dactyli of the walking legs. The following abbreviations are used in the text: Mxp (maxiliped), P1 (pereiopod 1, cheliped), P2- P4 (pereiopods 2-4, first to third walking legs), M (male), F (female) and ovig. (ovigerous).

All specimens, including the types of the new species, are deposited in the Museum national d'Histoire naturelle, Paris (MNHN), Florida Museum of Natural History, Gainesville (UF), the Natural History Museum, London (BMNH), the Australian Museum, Sydney (AM) and the collection of the National Taiwan Ocean University (NTOU).

DNA extraction, amplification and sequencing

Total genomic DNA was isolated from abdominal muscle tissue or pereiopods using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen). Three genes were amplified, two mitochondrial (16S rRNA and COI) and one from the nuclear genome (PEPCK). Only in some specimens representing the different mitochondrial clades was the nuclear gene amplified (see Table 1). Amplification was conducted using universal or newly designed primers (Table 2). Two different fragments of 16S rRNA were amplified. For the mitochondrial genes, PCR reactions were performed in a final volume of 50 µl. The PCR mix contained 2 µl of DNA template, 0.16 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer 10X, 3 µl of a 50 mM solution of $MgCl_2$, 0.5 µl of BSA (10 mg/ml), 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. Nuclear PCR reactions were conducted in a 50 µl final volume containing 2 µl of DNA template, 0.2 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer 10X, 3 µl

of a 50 mM solution of $MgCl_2$, 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. The cycling conditions for the mitochondrial genes were an initial denaturation step of 94ºC for 4 min followed by 39 cycles at 94ºC for 30 s, an annealing temperature of 45.5ºC (16S rRNA) or 45-50º (COI) for 1 min, 72ºC for 1 min, and a final extension at 72ºC for 10 min. For the nuclear gene, we performed an initial step of 94ºC for 3 min followed by 35 cycles at 94ºC for 30 s, 58-60º for 30 s, 72º for 1 min, and a final extension at 72ºC for 10 min. After PCR product purification by ethanol/sodium acetate precipitation, samples were cycle-sequenced using the ABI Prism BigDye Terminator, and subsequently run on an ABI 3730 Genetic Analyzer (Applied Biosystems, ABI). All sequences were deposited in GenBank under the accession numbers provided in Table 1. Specimens used for molecular analyses can be identified by a code (Allo) in the material examined of each species (Table 1).

Phylogenetic analysis

DNA sequences were edited using Sequencher 4.6 (Gene Codes, Ann Arbor, MI) and aligned manually in Se-Al version 2.0a11 (Rambaut, 1996). Phylogenies were constructed for each individual gene and congruence among the mitochondrial genes was tested using the incongruence length differences test (Mickevich & Farris, 1981; Farris *et al.*, 1994) implemented in PAUP* (v4.0 b10) along with the homogeneity partition test. Additionally, Bayesian tree topologies resulting from independent analyses of each of the genes were compared to find conflicting clades with a support greater than 95%, since the usefulness of the ILD test has been criticized (Barker & Lutzoni, 2002). Two different data sets were independently analyzed, one with information from both mitochondrial markers and the other with information from the nuclear gene.

The evolutionary molecular model that best fitted our data sets was selected using ModelTest 3.07 (Posada & Crandall, 1998) under the Akaike's Information Criterion (Akaike, 1974). This approach reduces the number of unnecessary parameters by penalizing more complex models (Nylander *et al.*, 2004). Phylogenetic reconstructions were obtained using the Bayesian Inference, maximum likelihood and maximum parsimony methods. Bayesian analyses were performed using Mr.Bayes version 3.1.2 (Huelsenbeck & Ronquist, 2001) with two independent runs of four Metropolis-coupled chains,

with 5 000 000 generations each, to estimate the posterior probability distribution. Model parameters were estimated as part of the analysis with uniform default priors. The program Tracer v1.4 (Rambaut & Drummond, 2003) was used to assess run convergence and determine the numbers of trees needed as burn-in. Trees prior to the log likelihood stabilization tree were discarded. To ensure that the analysis approached the optimal posterior distribution, an additional run was performed using the same conditions. Parsimony procedures were performed through a heuristic search using the TBR swapping algorithm, 10 random stepwise additions and treating indels as missing data using PAUP* (v4.0 b10). Maximum likelihood analyses were conducted in PHYML v2.4.4 (Guindon & Gascuel, 2003) using the evolutionary model selected by ModelTest 3.7 (Posada & Crandall, 1998). The robustness of the MP and ML inferred trees was tested by nonparametric bootstrapping (Felsenstein, 1985) with 1000 pseudoreplicates in each case. Bayesian posterior probabilities (BPPs) were used as a measure of the robustness of Bayesian trees. To test the monophyly of *Allogalathea*, two species of the genus *Galathea* were included in the phylogenetic analyses. These two specimens were provisionally denoted *Galathea sp1* and *Galathea sp2* in the phylogenetic trees.

Results

Systematics

Genus ***Allogalathea*** **Baba, 1969**

Allogalathea Baba, 1969: 5 (gender: feminine). — Poore, 2004: 231. — Baba *et al.*, 2009: 87.

Type species: *Allogalathea elegans* (Adams & White, 1848).

Diagnosis: Dorsal surface of carapace unarmed, with distinct transverse striae bearing fine but coarse setae, lateral margin medially convex with row of spines. Rostrum horizontal or slightly deflected, long, dorsally flattish, carinated ventrally, with 5-9 small lateral teeth and without supraocular spines. Tergites from abdominal segments unarmed. Telson relatively short, subdivision incomplete. Ocular peduncles short, cornea well pigmented. Orbit well delimited, lateral limit

rounded or blunty produced. Basal article of antennule with 3 terminal spines. Mxp3 ischium subtriangular in cross section, merus with flexor spines. P1 spinose, with setiferous squamae. P2-4 moderately short, with row of spines on dorsal crests of meri and carpi; flexor margin of dactyli with row of teeth each bearing corneous seta. Two pairs of male gonopods. Usually associated with crinoids.

Allogalathea babai n. sp.
(FIG. 1 - FIG. 6A)

Galathea elegans. — Miyake, 1938: 37, fig. 1, pl. 2, fig. D (in part). *Allogalathea elegans*. — Baba, 1969: 6, fig. 1 (in part). — Baba, 1977: 252 (in part). — Baba, 1979: 654, fig. 3 (in part). — Baba, 1982: 61. — Baba, 1988: 54 (in part). — Steene, 1990: 158, 320. — Gosliner *et al.*, 1996: 226, colour fig. 820 (in part). — Minemizu, 2000: 168, with 3 colour figs (in part). — Jones & Morgan, 2002: 133, colour fig. (no record). — Kawamoto & Okuno, 2003: 93, unnumbered colour figs (in part). — Poore, 2004: 231, pl. 13g (in part, compilation). — Kawamoto & Okuno, 2006: 93, unnumbered colour fig. (in part). — Macpherson, 2008: 289 (in part). — Baba *et al.,* 2008: 53 (in part, compilation), fig. 2C.

Material examined: Japan, Okinawa, Ie Island, 26º 43.474´N 127º 49. 899´E, 7 July 2004, 18-23 m: 1 M 4.1 mm, 1 ovig. F 6.6 mm (UF 7244, Allo7244).

Mariana Islands, Guam, Luminao ref., 21 May 1999, 10 m, under rubble: 1 M 3.1 mm, 1 ovig. F 3.9 mm (UF 277). — Pati Point, off Gorgonian, 28 July 2000, 24 m: 1 M 3.1 mm, 1 ovig. F 5.0 mm (UF 3856).

South China Sea. Macclesfield Bank, 24 m: 1 M 5.2 mm (BMNH 1892.8.28).

Indonesia. Rumphius Expedition II, East coast of Marsegu Island, 18 January 1975: 1 M 3.4 mm, on *Oxycomanthus bennetti* (MNHN-Ga 1133). — Rumphius Expedition II, Banda Sea, northern tip of Banda Sesar I., Banda Island, 30 January 1975: 1 F 5.6 mm, on *Oxycomanthus bennetti* (MNHN-Ga 1123).

Christmas Islands. North coast: 1 ovig. F 3.4 mm (UF 8069, Allo8069).

Vanuatu. SANTO. Stn DB33, 15°34.7'S, 167°13.8'E, 18 September 2006, 14-25 m: 1 M 2.4 mm (MNHN-Ga7353). — Stn FR1, 15°32.3'S, 167°13.1'E, 10 September 2006, 18-20 m: 1 ovig. F 8.4 mm (MNHN-Ga7354, Allo8).

New Caledonia. Lagoon, Touho, in front of Kohé, 08 September 1993: 21 M 2.9-4.8 mm, 8 ov. F 4.7-8.5 mm (MNHN-Ga7419), 1 ov. F 8.7 mm (MNHN-Ga7420, Allo17), 1 ov. F 7.6 mm (MNHN-Ga7421, Allo18), 1 ov. F 6.5 mm (MNHN-Ga7422, Allo19), 1 ov. F 4.7 mm (MNHN-Ga7423, Allo22), 1 M 4.7 mm (MNHN-Ga7424, Allo34), 1 ov. F 4.3 mm (MNHN-Ga7425, Allo36), 1 ov. F 5.4 mm (MNHN-Ga7429, Allo21). — 30 August 1993: 1 ov. F 6.9 mm, 1 F 2.9 mm (MNHN-Ga7355).

Touho Bank, 10 m: 1 M 2.5 mm (MNHN-Ga7426). — Touho Bank, 28 August 1993: 1 M 4.9 mm (MNHN-Ga7356,).

Chesterfield Islands. CORAIL 2. Stn CP90, 19°03'S, 158°56'E, 26 July 1988, 44-48 m: 1 M 6.1 mm, 1 ovig. F 8.0 mm (MNHN-Ga7357).

Loyalty Islands. Lifou Island. LIFOU 2000. Stn 1440, 20º47.2’S, 167º08.6’E, 11-16 November 2000: 15-35 m: 1 M 2.8 mm, 1 ov. F 3.8 mm (MNHN-Ga7358); 1 M 3.3 mm (MNHN-7359, Allo2); 1 ov.F 4.9 mm (MNHN-Ga7360). — 19 November 2000, dive: 1 M 3.4 mm (MNHN-Ga7361, Allo4).

Types: The ovigerous female of 5.4 mm postorbital carapace length, from New Caledonia (Lagoon, 8 September 1993, MNHN-Ga7429) was selected as the holotype. All the other specimens are paratypes.

Etymology: This species is dedicated to Dr. Keiji Baba of Kumamoto University, Japan, who described the genus *Allogalathea* and has greatly improved our knowledge of the taxonomy of squat lobsters.

Description: Carapace exclusive of rostrum 0.8-1.0 times long as broad; dorsal surface nearly horizontal from anterior to posterior and anterior cervical groove indistinct, posterior one distinct. Gastric region with 5-7 uninterrupted ridges, with or without scales between them, anterior first and second ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by slightly distinct cervical groove, followed by 6-9 transverse ridges mostly interrupted. Lateral margins with 8-9

spines: 2 spines in front of and 6-7 spines behind indistinct anterior cervical groove; first anterolateral, small, slightly posterior to level of lateral limit or orbit; second smaller than first, equidistant between anterolateral spine and anterior cervical groove; 3 spines on anterior branchial region, and 3-4 spines on posterior branchial margin, last small. Rostrum twice as long as broad with 8-9 small lateral teeth, length 0.9 that of carapace and dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 1A).

Pterygostomian flap rugose with sparse setae, anterior margin bluntly produced.

Sternal plastron 0.8 times long as broad, lateral limits divergent posteriorly. Sternite 3 twice broad as long, anterior margin with minute median notch. Sternite 4 2.7 times longer and 2.7 times broader than preceding sternite, 0.5 times long as broad; sternites 4 to 5 with some transverse ridges bearing setae (Fig. 1B).

Abdominal somites 2-4 each with 3-4 uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with 2 uninterrupted ridges; somite 6 with 2 uninterrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with blunt distomesial process nearly reaching distal margin of article 2. Article 2 with distolateral spine as long as distomesial, barely reaching midlength of article 3, sometimes additional mesial spine. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 1C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 23-27 denticles. Merus slightly longer than ischium, with 2 strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin usually with 3-4 small spines (Fig. 1D).

P1 squamous, 2.9 (males), 2.6-2.7 (females) times carapace length, subcylindrical, most dorsal squamae with some small spinules and dense long setae. Merus 0.5-0.8 times length of carapace, 1.6-1.9 times as long as carpus, with row of mesial and distodorsal spines. Carpus 0.5-0.6 length of palm, 1.1-1.4 times longer than broad, lateral and mesial margins subparallel, with row of spines along mesial and distodorsal margins. Palm 1.8-2.4 times longer than

broad, lateral and mesial margins straight or slightly convex in adult specimens; mesial row of spines, lateral margin with row of spines continuing on to whole lateral margin of fixed finger and most scales on dorsal surface with spinules. Fingers 0.7-0.9 as long as palm, distally crossing when closed; opposable margins nearly straight; mesial margin of movable finger with 2-3 subterminal spines and a few dorsomesial spinules (Fig. 1E).

P2-4 squamous, broad relative to length, weak in armature, moderately slender, somewhat compressed. Scales with dense short setae. Length of P2 1.7-1.9 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 length of P2 merus, P4 merus 0.8-0.9 length of P3 merus); P2 merus 0.6-0.7 carapace length, 3.2 times long as broad, 1.3-1.4 times longer than P2 propodus. Dorsal margins of meri only have a distodorsal spine and sometimes a row of small proximally diminishing spines on P2-3, unarmed on P4; ventrolateral margins with strong terminal spine.

Carpi with some dorsal spines; flexor distal margins with very small distal spine. Propodi subequal in length on P2 and P3, slightly shorter on P4, 4.0-4.2 times long as broad on P2; extensor margin unarmed; flexor margin with 6-7 slender movable spines. Dactyli subequal in length, 0.5-0.7 times length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by 5 obsolescent teeth, each with seta-like movable spine (Fig. 1F, 1G, 1H).

Epipods present on P1 and sometimes also on P2-3.

Colour: Body colour usually brown or orange, with a middle longitudinal whitish or yellowish broad stripe flanked by narrow dark brown stripes on each side (pattern 2) (Baba, 1969, 1979). P1-4 brown, orange or yellow; individuals with dark brown have a P1 white distal part of fingers, sometimes with whitish or yellowish dorsal stripe along merus, carpus and hand.

Remarks: The colour pattern of *A. babai* n.sp. is clearly different to the one exhibited by the other species (see below). All specimens of *A. babai* n. sp. have a brown colour on the body and pereiopods and a median longitudinal white broad stripe flanked on either side by a narrow dark brown stripe. Moreover, the new species has a variable number of epipods on the

pereiopods, suggesting that this character is not useful for species discrimination within the genus *Allogalathea* (see also *A. elegans*).

Allogalathea babai n. sp. is closely related to *A. elegans* in that both have a moderately long rostrum with spinules in most scales on the dorsal surface of the P1 palm. However, both species can be easily differentiated on the basis of other characters (see Remarks under *A. elegans*).

Distribution and habitat: Japan, Philippines, Mariana Islands, Guam, South China Sea, Christmas Islands, Indonesia (East coast of Marsegu Island, Banda Sea, Banda Island), Vanuatu, New Caledonia, Chesterfield and Loyalty Islands, Dampier Archipelago, W Australia. Depth: 10-48 m, usually on crinoids (*Oxycomanthus bennetti*).

Allogalathea elegans (Adams & White, 1848)
(FIG. 2 - FIG. 3 - FIG. 6B)

Galathea elegans Adams & White, 1848: pl. 12, fig. 7. — Balss, 1913: 4, figs 2-3. — Potts, 1915: 83, fig. 4, pl. 1, fig. 5. — Miyake, 1938: 37 (in part). — Melin, 1939: 77, figs 48-53 (probably in part). — Barnard, 1950: 487, figs 91, i-k. — Miyake & Baba, 1967: 228, fig. 3 (with doubt). — Lewinsohn, 1969: 123, fig. 24. — Healy & Yaldwyn, 1970: 67, pl. 31 (no record).

Galathea longirostris Dana, 1852: 482 (type lost; type locality: Fiji Islands, 18 m). — Dana, 1855: pl. 30, fig. 11. — Southwell, 1906: 220.

Galathea longirostris Yokoya, 1936: 138, fig. 6 (holotype, female, lost; type locality: Misaki, Sagami Bay, Japan) (not *G. longirostris* Dana, 1852).

Galathea deflexifrons Haswell, 1882: 761. — Haswell, 1882: 163.

Galathea grandirostris Stimpson, 1858: 90 (type lost; type locality: Kagoshima Bay, Japan, 9 m). — Stimpson, 1907: 234. — Henderson, 1888: 119, pl. 12, fig. 3. — Borradaile, 1900: 421.

Galathea (?) *grandirostris.* — Southwell, 1906: 221.

Allogalathea elegans. — Baba, 1969: 6, fig. 1 (in part). — Haig, 1973: 275 (in part). — Haig, 1974: 447 (in part). — Baba, 1977: 252 (in part). — Baba, 1979: 654, fig. 3 (in part). — Baba, 1988: 54 (in part). — Baba, 1990: 950. — Tirmizi & Javed, 1993: 27, figs 12, 13 (with doubt). — Gosliner *et al.*,

1996: 226, fig. 820 (in part). — Wu *et al.*, 1998: 84, figs 6, 12C. — Minemizu, 2000: 168, with 3 figs (in part). — Kawamoto & Okuno, 2003: 93, unnumbered figs (in part). — Poore, 2004: 231, fig. 63e, pl. 13g (in part, compilation). — Kawamoto & Okuno, 2006: 93, unnumbered fig. (in part). — Macpherson, 2008: 289 (in part). — Poore *et al.*, 2008: 18. — Baba *et al.,* 2008: 53, fig. 2B.

Material examined: Madagascar. Nosy Komba, NW side, 13.4462ºS, 48º3316ºE, 26 May 2008, 0-12 m: 1 M 5.3 mm, 1 ovig. F 7.0 mm, 1 F 2.4 mm (UF 14196).

Between Nosy Be and Nosy Tanikely, muddy lagoon, crinoid, 13.4572ºS, 48.2484ºE, 21 May 2008, 24-25 m: 1 F 4.6 mm (UF 14641).

Nosy Be. Stn 10, dive, 26 m, P. Laboute coll. 1994: 2 ovig. F 5.1-5.3 mm (MNHN-Ga7372, Allo43).

S coast. VAUBAN. Stn CH74, 25º04.8'S, 46º55.7'E, 04 March 1973, 28 m: 5 M 2.8-5.2 mm, 1 ovig. F 5.0 mm, 1 F 3.1 mm (MNHN-Ga 726).

NW coast, 12º49.5'S, 48º30'E, 2 August 1973, 55 m: 2 M 4.6-5.3 mm, 1 F 2.5 mm (MNHN-Ga 1503, 2226, 2227).

W coast, FAO 26. 17º05'S, 43º50'E, 26 September, 40-46 m: 1 ovig. F 5.9 mm (MNHN-Ga 1486).

NW coast, near Tanikely, 13º28'S, 48º12'E, 26 February 1971, 28 m: 1 ovig. F 5.4 mm (MNHN-Ga 725).

Mitsio Islands, February 1960, 60 m: 3 M 4.1-5.7 mm, 6 ovig. F 4.4-6.1 mm, 2 F 5.2-6.6 mm (MNHN-Ga 2240).

Reunion Island. MD32 Cruise. Stn CP127, 20º52.0'S, 55º37.1'E, 02 September 1982, 90 m: 1 ovig. F 5.6 mm (MNHN-Ga4583).

Mozambique. MAINBAZA. Stn CP3132, 35º01'51''S, 25º11'24''E, 101-102 m, Richer de Forges & Corbari coll., 10.04.2009: 1 ovig. F 8.3 mm (MHN-Ga7373).

Gulf of Suez. Dolfus coll., 8 December 1928: 1 M 4.1 mm (MNHN-Ga 762).

Taiwan**.** Longdong, Taipei County, 21 July 1999: 1 F 2.6 mm (NTOU). Gushan fishing port, Kaohsiung City, 14 January 1985: 1 M 5.2 mm (NTOU). Stn CP02, 23°38.3'N, 119°53.2'E, 27 July 2000, 83-95 m: 1 F 5.2 mm (NTOU).

Philippines. Corregidor Island: 1 M 4.1 mm, 1 F 5.0 mm (types, BMNH 1843, see below).

MUSORSTOM 3. Stn DR104, 13°56'N, 120°22'E, 1 June 1985, 13 m: 1 M 2.1 mm (MNHN-Ga7374).— Stn DR117, 12°31'N, 120°39'E, 3 June 1985, 92-97 m: 2 ovig. F 3.9 mm (MNHN-Ga7396) and 5.1 mm (MNHN-Ga7397).— Stn CP121, 12°08'N, 121°17'E, 3 June 1985, 73-84 m: 1 M 3.1 mm, 2 F 2.8-3.5 mm (MNHN-Ga7375), 1 M 4.5 mm (MNHN-Ga7376, Allo39), 1 M 3.3 mm (MNHN-Ga7377).— Stn CP142, 11°47'N, 123°01'E, 6 June 1985, 26-27 m: 2 M 4.3-5.6 mm, 2 ovig. F 3.7-4.7 mm (MNHN-Ga7378).

Indonesia. East coast of Marsegu Is., 18 January 1975, on *Comanthina schlegeli*, 1 M 2.5 mm, 1 ovig. F 4.1 mm (MNHN-Ga 1127); 1 M 3.0 mm on *Oxycomanthus bennetti* (MNHN-Ga 1133).

Lilinta Bay, across from Lilinta village, Misool Is., 23 January 1975, on *Comanthina schlegeli* and *C. parvicirrus*: 3 M 2.2-3.6 mm (MNHN-Ga 1128, 1131, 1132).

Off Museha and Wayuta estuaries, Seleman Bay, north coast of Seram (Ceram), 19 January 1975, on *Comanthina parvicirrus* and *Stephanometra spicata*: 2 M 2.0-2.5 mm, 1 ovig. F 3.3 mm (MNHN-Ga 1126, 1130).

Banda Island, 30 January 1975: 1 M 3.8 mm (MNHN-Ga 1120).

Southern entrance between Gunung Api Is. and Bandanaira, on *Comanthina schlegeli*, 29 January 1975: 1 M 3.8 mm, 1 F 4.2 mm (MNHN-Ga 1121).

Across from Kotasirih village, Kailakat Bay, Gorong Island, 26 January 1975, on *Capillaster multiradiatus*: 1 M 5.5 mm (MNHN-Ga 1119). 25 January 1975, on *Oxycomanthus bennetti*, 1 M 2.0 mm (MNHN-Ga 1124).

Across from Kotasirih village, Kailakat Bay, Gorong Island, 27 January 1975, on *Comanthina schlegeli*: 1 ovig. F 5.0 mm (MNHN-Ga 1122).

Tapalol Is., off Biga Bay, Missol Is., 24 January 1975, on *Stephanometra spicata*: 1 M 1.6 mm (MNHN-Ga 1129).

CORINDON. Stn DR258, 01º56.8’S, 119º17.3’E, 6 November 1980, 30 m: 1 M 3.7 mm (MNHN-Ga7379,).

Vanuatu. SANTO. Stn FR1-CF2, 15°32.3'S, 167°13.1'E, 10 September 2006,18-20 m: 1 M 4.1 mm (MNHN-Ga7380, Allo11).— Stn FR06, 15°32.6'S, 167°16.9'E, 13 september 2006, 3-37 m : 1 M 4.2 mm, 1 ov. F 5.1 mm (MNHN-Ga7395). — Stn ZR4, 15°33.1'S, 167°09.6'E, 17 September 2006, 0-45 m: 1 M 3.9 mm (MNHN-Ga7381, Allo15), 1 ovig. F 4.7 mm (MNHN-Ga7382, Allo9). — Stn AT13, 15°27.8'S, 167°15.7'E, 19 September 2006, 146-153 m: 1 ovig. F 3.7

mm (MNHN-Ga7383).— Stn AT14, 15°23.7/24'S, 167°12.9/13.5'E, 19 September 2006, 102-120 m: 2 ovig. F 3.3 (MNN-Ga7384) and 4.6 mm (MNHN-Ga7385, Allo31).— Stn EP22, 15°37.3/37.4'S, 167°05.8/06.0'E, 21 September 2006, 78-91 m: 1 M 3.2 mm (MNHN-Ga7386).— Stn FR26, 15°31.7'S, 167°09.5'E, 21 September 2006, 3-33 m: 1 M 3.5 mm, 1 F 1.8 mm (MNHN-Ga7387).— Stn AT40, 15°23.4'S, 167°12.7'E, 27 September 2006, 81-94 m: 1 ovig. F 4.2 mm (MNHN-Ga7388).— Stn AT44, 15°36.5'S, 167°02.7'E, 29 September 2006, 86-118 m: 1 ovig. F 5.8 mm (MNHN-Ga7389, Allo13).— Stn DB80, 15°37.1'S, 167°07.5'E, 02 October 2006, 18 m: 1 M 2.6 mm, 2 F 2.2-3.0 mm (MNHN-Ga7390).— Stn AT75, 15°37.0/37.3'S, 167°09.2/09.6'E, 10 October 2006, 52-66 m: 1 M 2.6 mm, 2 F 2.9-4.0 mm (MNHN-Ga7391).— Stn AT81, 15°31.5'S, 167°11.9'E, 12 October 2006, 46-55 m: 1 ovig. F 6.0 mm (MNHN-Ga7392, Allo7).— Stn AT82, 15°31.6'S, 167°12.4'E, 12 October 2006, 58-59 m: 1 ovig. F 4.9 mm (MNHN-Ga7393, Allo6). — Stn AT84, 15°32.4'S, 167°14.3'E, 12 October 2006, 71-104 m: 1 ovig. F 6.0 mm (MNHN-Ga7394, Allo14).

New Caledonia. Lagoon, 30 August 1993: 2 M 3.0-4.1 mm, 2 ovig. F 3.0-4.2 mm (MNHN-Ga7398).

In front Kohe, 08 September 1993, 15 m: 6 M 3.5-4.6 mm, 8 ov. F 3.0-5.3 mm, 1 F 3.8 mm (MNHN-Ga7428),1 ov. F 5.4 mm (MNHN-Ga7399, Allo20) + 1 ov. F 5.2 mm (MNHN-Ga7400, Allo35) + 1 M 4.5 mm (MNHN-Ga7401, Allo33) .

Touho Bank, 28 August 1993: 3 M 2.1-4.5 mm, 2 ovig. F 3.1-5.6 mm, 7 F 1.8-3.0 mm (MNHN-Ga7402; Ga7403, Allo25; Ga7404, Allo23; Ga7405).

Touho Channel, 04 September 1993, 52 m: 1 M 4.7 mm, 2 ovig. F 5.7-6.0 mm (MNHN-Ga7406). — 07 September 1993, 56 m: 2 F 4.0-5.7 mm 2 F 4.0-5.7 mm + 1 M 3.1 mm (MNHN-Ga7427), 1 F 5.7 mm (MNHN-Ga7407, Allo29).

Touho Bank. 20º44.20’S, 165º14’E, 15/16 September 1993: 2 M 4.2-4.6 mm, 2 ovig. F 4.3-5.3 mm (MNHN-Ga7408).

Touho (Kohé), Opération MONTROUZIER, dive, 15 m, 07 september 1993 : 1 M 3.9 mm, 1 ov. F 4.4 mm. (MNHN-Ga7416) ; same cruise, same date, 20°48.93’S, 166°16.80’E, 55-60 m: 1 F 2.3 mm (MNHN-Ga7417).

Ilot Canard, 22º09.2’S, 166º21.7’E, 20 m: 2 M 3.9-4.2 mm, 2 ovig. F 3.9-5.2 mm (MNHN-Ga7409).

Grand Recif Sud. Stn 302, 22º38’S, 166º49’E, 17 m: 1 M 4.1 mm, 1 ovig. F 7.1 mm (MNHN-Ga7410).

Plotmatre , perhaps Ilot Maitre. 22º19.35’S, 166º25.85’E, 11 November 1995, 20 m: 1 ov. F 5.3 mm (MNHN-Ga7411).

Gail Bank, 1970, 30 m: 1 M 5.9 mm (MNHN-Ga 523).

Chesterfield islands. CORAIL 1. Bank Landsdowne, August 1988: 2 M 3.2-4.3 mm, 2 ovig. F 5.1-5.7 mm (MNHN-Ga7414).

CORAIL 2. Stn CP25, 20°25'S, 161°05'E, 22 July 1988, 67-70 m: 1 M 2.3 mm (MNHN-Ga7415).

E Australia. Albany Passage, Queensland: 1 specimen dry 4.5 mm (type of *Galathea deflexifrons* Haswell) (AM P3885).

Types: The female of 5.0 mm postorbital carapace length from Philippines, Corregidor Island (BMNH, 1843) has been selected as the lectotype. The male specimen of 4.1 mm has been considered a paralectotype

Description: Carapace, exclusive of rostrum, as long as broad; dorsal surface nearly horizontal from anterior to posterior, with distinct transverse striae bearing fine but coarse setae and cervical groove slightly distinct. Gastric region with 4-5 uninterrupted and 1-2 interrupted ridges, first anterior and second uninterrupted, ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by distinct cervical groove, followed by 3-5 transverse ridges, last one interrupted. Lateral margins with 9 spines: 2 spines in front of and 7 spines behind anterior cervical groove; first anterolateral, small, slightly posterior to level of lateral limit of orbit; second slightly smaller than first, equidistant between anterolateral spine and anterior cervical groove; 3 spines on anterior branchial region, and 4 spines on posterior branchial margin, decreasing in size posteriorly. Rostrum 2.0-2.3 times long as broad with 7-8 small lateral teeth, length subequal to that of carapace; dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 2A).

Pterygostomian flap setiferous striae, anterior margin bluntly produced.

Sternal plastron 0.8 times as long as broad, lateral limits divergent posteriorly. Sternite 3 three times as broad as long, anterior margin with minute median notch. Sternite 4 4.6 times longer and 2.5 times broader than preceding sternite, 0.6 times long as broad; sternites 4 to 5 with a few short transverse

ridges bearing short setae (Fig. 2B).

Abdominal somites 2-4 each with 3 uninterrupted transverse ridges on tergite, usually without scales in between; second ridge interrupted medially in some specimens; somite 5 with 2 uninterrupted ridges and few scales, somite 6 with 2 interrupted ridges and few scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with blunt distomesial process reaching or overreaching end of article 2. Article 2 with distolateral spine larger than distomesial, nearly reaching end of article 3. Article 3 with distinct distomesial spine reaching end of article 4. Article 4 unarmed (Fig. 2C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 20-23 denticles. Merus slightly longer than ischium, with 2 strong spines of subequal size on flexor margin, proximal one located slightly distal to midlength, distal one at terminal end; extensor margin unarmed or with 2-3 small spines (Fig. 2D).

P1 squamous, 2.2-3.0 times carapace length, subcylindrical, lateral and mesial margins straight in adult specimens; each squama usually with 1 spinule and some long setae. Merus 0.7-0.8 times length of carapace, 1.3-1.4 times as long as carpus, with spines on mesial and distodorsal margins. Carpus 0.7-0.9 length of palm, 1.8-2.2 times longer than broad, lateral and mesial margins subparallel; mesial margin with row of spines. Palm 2.2-2.6 times longer than broad, lateral and mesial margins subparallel; mesial row of spines, lateral margin with row of spines continuing on to whole lateral margin of fixed finger and most scales on dorsal surface with spinules. Fingers 0.8 length of palm, distally crossing when closed; opposable margins nearly straight, mesial margin of movable finger with 2-3 subterminal spines (Fig. 2E).

P2-4 squamous, relatively slender, somewhat compressed, with short setae on each squama. P2 1.5-1.8 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus 0.6-0.7 carapace length, 4.0-4.2 times long as broad, 1.3-1.4 times longer than P2 propodus. Dorsal margins of meri with distodorsal spine and row of well-developed proximally diminishing spines on P2-3, unarmed or with some minute spines on P4; ventrolateral margins with strong

terminal spine. Carpi with some dorsal spines on P2 and P3, unarmed on P4; flexor distal margins with small spine. Propodi slightly longer on P3 than on P2, slightly shorter on P4 than on P2. P2 propodus 4.3 times long as broad, 1.9 times longer than P2 dactylus; extensor margin unarmed; flexor margin with 6-10 slender movable spines. P2-3 dactyli subequal in length, slightly longer than P4 dactylus, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by 4-5 obsolescent teeth, each with seta-like movable spine (Fig. 2F, 2G, 2H).

Epipods present or absent on P1, absent on P2-3.

Colour: The species has several possible body colour patterns: either uniformly dark (red, blackish purple, orange or brown), or dark with either two narrow light stripes, or alternating longitudinal dark and light stripes (patterns 1, 3 and 4 of Baba, 1979), whose number and width varies. Other colour patterns include a narrow lighter stripe in the middle of each dark stripe. Pereiopods also show variable coloration: P1 uniformly dark or with longitudinal light dorsal stripe along merus, carpus and palm, finger tips light; some specimens with P1 uniformly dark and fingers whitish. P2-4 uniformly dark or pale on distal portion of carpus, distal portion of propodus and entire dactylus; in some specimens, P2-4 meri dark, and carpi, propodi and dactyli whitish.

Remarks: A number of different taxa as *Galathea longirostris* Dana, 1852; *G. grandirostris* Stimpson, 1858; *G. deflexifrons* Haswell, 1882; and *G. longirostris* Yokoya, 1936 have been judged to be junior synonyms of *G. elegans* Adams & White, 1848 (Ortmann, 1894; Grant & McCulloch, 1906, among others). However, Baba (1969) recommended that previous records should be revised, confirming the presence or absence of epipods on P1-3. It should be noted that Haig (1973) pointed out that the status of three of these species could not be resolved because their types are no longer extant (see Material examined).

The description and illustration by Dana (1852) suggest that *G. longirostris* is very close to *A. elegans*, the rostrum of both having 5 to 6 small spines on each side, and the body background colour of the body of both is purplish black, with two whitish stripes. The description of *G. grandirostris* by Stimpson (1858) is very brief and not illustrated and includes a purplish black body background

colour with two light stripes. A similar short description of *G. deflexifrons* was provided by Haswell (1882), who, as a distinctive character, pointed out that the rostrum is deflected. However, examination of the type species of *G. deflexifrons* Haswell, 1882 (in photographs provided by the Australian Museum, Sydney) indicates it is a junior synonym of *A. elegans*. The description of *G. longirostris* by Yokoya (1936), a junior homonym of *G. longirostris* Dana, 1852, is more detailed and includes illustrations (only one female was collected). The body background colour has alternating brown and white stripes, and corresponds well with the original illustration of *A. elegans*.

Considering the impossibility of knowling the exact status of *Galathea longirostris* Dana, 1852, *G. grandirostris* Stimpson, 1858, and *G. longirostris* Yokoya, 1936, we select the syntype female illustrated in Figure 3 as the lectotype of *G. elegans* Adams & White, 1848. This lectotype is designated as the neotype of Dana´s, Stimpson´s and Yokoya´s records and therefore these names should be considered objective junior synonyms of *G. elegans* Adams & White, 1848.

Allogalathea elegans is close to *A. babai* n. sp. but the two can be distinguished by the following characters:

- The walking legs (P2-4) are shorter and more slender in *A. babai* n. sp. than in *A. elegans*. The P2 merus is about 3 times longer than high in the new species, whereas the P2 merus is 4 times longer than high in *A. elegans*.
- The dorsal margin of the P2-3 meri is usually unarmed or has small spines in *A. babai* n. sp., yet has well-developed spines in *A. elegans*.
- The squamae on the dorsal side of P1 have several spinules and numerous long setae in *A. babai* n. sp., whereas these squamae have only one spinule and a few long setae in *A. elegans*. These squamae are denser in *A. babai* n. sp. than in *A. elegans*.
- Epipods are always present on P1 and sometimes on P2-3 in *A. babai* n. sp., instead of being present on P1 only or absent on all pereiopods as in *A. elegans*.

Furthermore, *A. babai* n. sp. has a middle longitudinal light broad stripe which is never found in *A. elegans*.

Distribution and habitat: Mozambique, Red Sea, Madagascar, Taiwan, Philippines, Indonesia (Banda and Celebes Seas), Vanuatu, New Caledonia and Chesterfield islands. Subtidal to 120 m; usually on crinoids, e.g. *Capillaster multiradiatus, Comanthina schelegeli, C. parvicirrus, Oxycomanthus bennetti*, *Stephanometra spicata*.

The distribution range of *A. elegans* is probably wider and its occurrence in the areas cited (material not examined), e.g. South Africa, Sri Lanka, Bay of Bengal, Japan, western and southwestern Australia, Queensland, Great Barrier Reef , Fiji, among others, needs confirmation.

***Allogalathea inermis* n. sp.**
(FIG. 4 - FIG. 6C)

Galathea elegans. — Miyake, 1938: 37, fig. 1, pl. 2, fig. E (in part). — Melin, 1939: 77, figs 48-53 (in part). — Utinomi, 1956: 63, pl. 32, colour fig. 4.
Allogalathea elegans. — Baba, 1969: 6, fig. 1 (in part) — Baba, 1979: 654 (in part). — Baba, 1988: 54 (in part).

Material examined: Mozambique. MAINBAZA. Stn DW3168, 35°3’ E, 26°12’ S, 87-90 m, Richer de Forges & Corbari coll., 16 april 2009: 1 M 6.4 mm (MNHN-Ga7362, Allo42).

Thailand. Phuket. Coral reefs: 1 M 3.9 mm (MNHN-Ga7363, Allo28), 1 F 4.9 mm (MNHN-Ga7364, Allo27).

Indonesia Rumphius Expedition II, in front of Kotasirih village, Kailakat Bay, Gorong Island, 25 January 1975: 1 M 1.7 mm, 1 F 1.8 on *Himerometra robustipinna* (MNHN-Ga 1125).

Vanuatu. Espiritu Santo, SANTO 2006. Stn NR8, 15°35.7'S, 167°07.4'E, 15 September 2006, 11 m: 1 M 3.1 mm (MNHN-Ga7365, Allo30), 1 ovig. F 3.6 mm (MNHN-Ga7366, Allo12).

New Caledonia. Touho Bank, 28 August 1993: 1 M 3.8 mm, 1 ovig. F 5.1 mm, 1 F 3.5 mm (MNHN-Ga7367) .— Touho, 10 m, 1 ov. F 4.4 mm (MNHN-Ga7418).

Lagoon. Across from Kohe, 08 September 1993: 1 M 5.1 mm (MNHN-Ga7368, Allo32).

New Caledonia. SMIB 5. Stn DW100, 23°22.90'S, 168°05.20'E, 14 September 1989, 80-120 m: 1 ovig. F 7.3 mm (MNHN-Ga7369, Allo3).

Chesterfield Islands. CORAIL 2. Stn CP7, 20°52'S, 161°37'E, 20 July 1988, 63-64 m: 1 M 4.5 mm, 1 ovig. F 4.8 mm (MNHN-Ga7370). — Stn CP90, 19°03'S, 158°56'E, 26 July 1988, 44-48 m: 1 ovig. F 4.9 mm (MNHN-Ga7371).

Types: The ovigerous female of 7.3 mm postorbital carapace length, from New Caledonia (SMIB 5, Stn DW100, MNHN-Ga7369) has been selected as the holotype. All the other specimens are paratypes.

Etymology: From the Latin *inermis* (unarmed), referring to the absence of spinules on most squamae of P1.

Description: Carapace, exclusive of rostrum 0.9 times long as broad; dorsal surface nearly horizontal from anterior to posterior and cervical groove slightly distinct. Gastric region with 5-6 uninterrupted and 2-3 interrupted ridges, usually with some scales between them, anterior first, third and fourth uninterrupted ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to fifth marginal spines, preceded by cervical groove, followed by 5-6 transverse ridges. Lateral margins with 8-9 spines: 2 spines in front of and 6 spines behind cervical groove; first anterolateral, small, slightly posterior to level of lateral limit of orbit; second smaller than first, equidistant between anterolateral spine and anterior cervical groove; 3 spines on anterior branchial region, and 4 spines on posterior branchial margin, last very small. Rostrum 1.3-1.6 times long as broad, with 8-9 lateral small teeth, length 0.7 that of carapace, dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 4A).

Pterygostomian flap with some ridges, anterior margin bluntly produced.

Sternal plastron 0.8 times long as broad, lateral limits divergent posteriorly.

Sternite 3 2.6 times broad as long, anterior margin with small median notch. Sternite 4 2.6 times longer and 2.4 times broader than preceding sternite, 0.4 times long as broad; sternites 4 to 5 with some transverse ridges bearing long setae (Fig. 4B).

Abdominal somites 2-4 each with 2-3 uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with 2 uninterrupted ridges, somite 6 with 2 interrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle hardly visible from dorsal view, with distomesial spine reaching midlength of article 2. Article 2 with distolateral spine as long as distomesial, overreaching midlength of article 3, sometimes additional mesial spine. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 4C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 19-24 denticles. Merus slightly longer than ischium, with 2 strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin with 3-4 spines (Fig. 4D).

P1 squamous, 2.0-2.5 times carapace length, subcylindrical, most dorsal squamae lack spinules and with numerous long setae. Merus 0.8 times length of carapace, 1.4-1.6 times long as carpus, with row of mesial and distodorsal spines. Carpus 0.6-0.7 length of palm, 1.5-1.6 times longer than broad, lateral and mesial margins subparallel, with row of spines along mesial and distodorsal margins. Palm 1.7-1.8 times longer than broad, lateral and mesial margins convex in adult males (slightly in females); mesial margin with row of spines, lateral margin with row of spines continuing on to whole lateral margin of fixed finger and most scales on dorsal surface without spinules. Fingers as long as palm, distally crossing when closed; opposable margins nearly straight; mesial margin of movable finger with 2-3 subterminal spines (Fig. 4E).

P2-4 squamous, weak in armature, relatively slender, somewhat compressed, with long setae. P2 1.5 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.9 times length of P3 merus); P2 merus 0.5-0.6 carapace length, 3.5 times as long as

broad, 1.2-1.5 times longer than P2 propodus. Dorsal margins of meri with distal spine and row of small proximally diminishing spines on P2-3, nearly unarmed on P4; ventrolateral margins with strong terminal spine. Carpi with some dorsal spines on P2 and P3, unarmed on P4; flexor distal margins with very small distal spine. Propodi subequal in length on P2 and P3, slightly shorter on P4, 3.3-3.4 times as long as broad on P2; extensor margin unarmed; flexor margin with 6-7 slender movable spines. Dactyli subequal in length, 0.6 times length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by 4-5 obsolescent teeth, each with seta-like movable spine (Fig. 4F, 4G, 4H).

Epipods present on P1, absent on P2-3.

Colour: Three patterns have been observed: carapace and abdomen uniformly dark, usually brown or red (pattern 1 of Baba, 1979), dark brown with two narrow light stripes (pattern 3 of Baba, 1979), and alternating dark and light longitudinal stripes (pattern 4 of Baba, 1979). Pereiopods uniformly dark (red or brown) or yellowish.

Remarks: *Allogalathea inermis* n. sp. is easily differentiated from the other closely related species (*A. babai* n. sp. and *A. elegans*) according to the following features:

- The rostrum is shorter in *A. inermis* n. sp. (1.3-1.6 times longer than wide) than in *A. babai* n. sp. and *A. elegans* (2.0-2.3 times longer than wide).
- The squamae on the dorsal surface of the P1 palm are mostly unarmed in *A. inermis* n. sp., whereas these squamae have at least one spinule in *A. babai* n. sp. and *A. elegans.*
- The mesial and lateral margins of P1 palm are convex in the adult males of *A. inermis* n. sp., whereas these margins are straight in *A. babai* n. sp. and *A. elegans.*

Distribution and habitat: Mozambique, Japan, Thailand, Indonesia (Gorong Island), Vanuatu, New Caledonia and Chesterfield Islands, between 44 and 120 m. Usually living on crinoids (*Oxycomanthus bennetti* and *Himerometra*

robustipinna).

Allogalathea longimana n. sp.
(FIG. 5 - FIG. 6D)

Galathea elegans — Haswell, 1882: 163. — Grant & McCulloch, 1906: 50, pl. 4, figs 6, 6a.
Allogalathea elegans — Miyake, 1982: 149, pl. 50, colour fig. 5.

Material examined: Philippines. MUSORSTOM 3. Stn CP97, 14°01'N, 120°19'E, 1 June 1985, 189-194 m: 1 M 6.7 mm (MNHN-Ga7430, Allo44).— Stn CP107, 14°02'N, 120°28'E, 2 June 1985, 111-115 m: 1 M 3.8 mm (MNHN-Ga7431, Allo46), 1 ovig. F 6.5 mm (MNHN-Ga7432, Allo38).— Stn CP124, 12°03'N, 121°35'E, 4 June 1985, 120-123 m: 2 M 6.6-7.2 mm, 2 ovig. F 6.3-7.5 mm (MNHN-Ga7433 & MNHN-Ga7434, Allo45).

Types: The ovigerous female of 6.5 mm postorbital carapace length from Philippines (MUSORSTOM 3, Stn CP107, MNHN-Ga7432) has been selected as the holotype. The other specimens are paratypes.

Etymology: From the Latin *longus* (long) and *manus* (hand), referring to the long cheliped (P1) and P1 palm, a character that separates this species from the other three species in this genus.

Description: Carapace, exclusive of rostrum, as long as broad; dorsal surface nearly horizontal from anterior to posterior and cervical groove very shallow. Gastric region with 5-6 uninterrupted ridges and 2-3 interrupted ridges, usually without scales between them, anterior first and third ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by very shallow cervical groove, followed by 6-9 transverse ridges, mostly interrupted. Lateral margins with 8-10 spines: 2 spines in front of and 6-8 spines behind indistinct anterior cervical groove; first anterolateral, well-developed, slightly posterior to level of lateral limit of orbit; second smaller than first, equidistant between anterolateral spine and anterior

cervical groove; 3 spines on anterior branchial region, and 3-5 spines on posterior branchial margin, decreasing in size posteriorly. Rostrum moderately long with 8-10 small lateral teeth, 1.8 times longer than broad, length 0.7 that of carapace, dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 5A).

Pterygostomian flap with some setigerous ridges, anterior margin ending in small spine.

Sternal plastron 0.8 times long as broad, lateral limits divergent posteriorly. Sternite 3 twice as broad as long, anterior margin with small median notch. Sternite 4 2.8 times longer and 2.8 times broader than preceding sternite, 0.5 times long as broad; sternites 4 to 5 with a few transverse ridges bearing short setae (Fig. 5B).

Abdominal somites 2-4 each with 4-5 uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with 2 uninterrupted ridges, somite 6 with 2 interrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with distomesial spine reaching midlength of article 2. Article 2 with distolateral spine clearly longer than distomesial, nearly reaching end of article 3. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 5C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 19-23 denticles. Merus slightly longer than ischium, with 2-3 strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin unarmed or with 2-3 small spines (Fig. 5D).

P1 squamous, 3.9-4.0 times carapace length, subcylindrical, lateral and mesial margins straight in adult specimens, most dorsal squamae unarmed or with 1-2 small spinules and long setae. Merus 1.1-1.3 times length of carapace, 1.3-1.6 times as long as carpus, with row of few spines along mesial and distodorsal margins. Carpus 0.6-0.7 length of palm, 3.8-4.0 times longer than broad, lateral and mesial margins subparallel, mesial and distodorsal margins with row of few spines. Palm 5.0-6.5 times longer than broad, dorsal surface without spinules; lateral and mesial margins subparallel, lacking spines. Fingers

0.4 times as long as palm, distally crossing when closed; opposable margins nearly straight; mesial margin of movable finger with 2-3 subterminal spines (Fig. 5E).

P2-4 squamous, slender, somewhat compressed, striae with long setae. P2 length 1.6-1.7 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus 0.6-0.8 times carapace length, 3.5-4.0 times long as broad, 1.3-1.5 times longer than P2 propodus. Dorsal margins of meri with distal and row of small proximally diminishing spines on P2-3, unarmed on P4 except distal spine; ventrolateral margins with strong terminal spine. Carpi with some dorsal spines; flexor distal margins with very small spine. Propodi slightly shorter on P4 than on P2 and P3, 4.0 times long as broad on P2 and P3; extensor margin unarmed; flexor margin with 6-8 slender movable spines. Dactyli subequal in length, half length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by 5-6 obsolescent teeth, each with seta-like movable spine (Fig. 5F, 5G, 5H).

Epipods present on P1.

Colour: Body with alternating longitudinal dark brown, white or yellow stripes (pattern 4 of Baba, 1979). The middle stripe is always dark brown. P1-4 brownish or yellowish.

Remarks: The species can be easily distinguished from the other three species of the genus according to the length of P1. The chelipeds (P1) are about 4 times the length of the carapace in *A. longimana* n. sp., with the palm about twice the finger length. In the other species, the length P1 is always less than 3 times the carapace length, with the palm as long as or slightly longer than the fingers.

Distribution and habitat: Japan, the Philippines and Queensland, between 36 and 194 m. Habitat unknown.

Key to species of the genus *Allogalathea*

1. P1 long, more than 3 times carapace length. Palm twice finger length……..…… ***A. longimana* n. sp.**

- P1 short, equal or less than 3 times carapace length. Palm as long or slightly longer than finger length

…….…….…… 2

2. Rostrum short, 1.3-1.6 times longer than wide. Most scales on dorsal surface of palm without spinules. Mesial and lateral margins of P1 palm slightly convex in adult specimens ……..…….. ***A. inermis* n. sp.**

- Rostrum moderately long, 2.0-2.3 times longer than wide. Most scales on dorsal surface of palm with spinules. Mesial and lateral margins of P1 palm straight or slightly convex in adult specimens…….……..... 3

3. P2-4 broad relative to length, P2 merus 3 times longer than height. Dorsal margin of P2-3 meri usually unarmed or with minute spines……
…….....…***A. babai* n. sp.**

4. P2-4 moderately narrow relative to length, P2 merus 4 times longer than height. Dorsal margin of P2-3 meri has well-developed spines……..
……..…….……... ***A. elegans***

Molecular analysis

Two mitochondrial markers were amplified in 43 specimens, and a nuclear gene amplified in only some specimens representing the different mitochondrial clades (Table 1). After alignment, the two mitochondrial genes gave rise to a sequence data set comprising 1540 base pairs. The two independent 16S rRNA fragments yielded 882 bp. Two regions between positions 245-280 and between 703-716 showed high variability and both required the insertion of gaps. For this gene, 577 characters were constant, 106 were parsimony uninformative, and 199 were parsimony informative. In the COI

sequence of 658 bp, 453 characters were constant, 35 were parsimony uninformative and 170 characters were parsimony informative.

The data set for the nuclear gene PEPCK comprised 598 characters, of which 537 were constant, 30 were parsimony uninformative and 31 were parsimony informative. No introns or indels were present in the sequences, but ambiguities such as double peaks in the chromatograms were detected, probably due to the heterozygosity of the specimens from which the sequence was derived. These positions were coded as ambiguities using the IUB symbols as M, S, Y, R, K or W and were present at several sites within single sequences.

The mitochondrial genes indicated four strongly divergent clades (designated *A. elegans*, *A. babai* n. sp., *A. inermis* n. sp. and *A. longimana* n. sp.) (Fig. 7). Molecular divergence among clades ranged from 8.40 to 12.06% for the 16S rRNA gene sequences and from 10.94 to15.53% for the COI gene (Table 3). The COI gene was generally more variable between and within species than 16S rRNA. Within *A. babai* n. sp., the specimen Allo8069 from the Christmas Islands showed an intraspecific mean divergence of 4.5% for both mitochondrial genes, which is fairly high compared to divergences among other specimens. The nuclear gene showed a molecular divergence of 0.5 to 3.5%. Highest divergence was observed between *A. babai* n. sp. and *A. longimana* n. sp. at 2.3-3.5% and lowest divergence between *A. elegans* and *A. inermis* n. sp. Lower variation in genetic divergence was detected within the groups in each species.

Phylogenetic inference

Data from the mitochondrial genes were combined in a single matrix because the incongruence length difference (ILD) test revealed no significant incongruence among gene partitions, and there were no strongly supported conflicting nodes among the tree topologies. The best- fit model selected using Modeltest was GTR+G (General Time-Reversible model, Lavane *et al.*, 1984; Rodríguez *et al.*, 1990), which rendered a γ-shape parameter of 0.1702 for the ML analysis. Base frequencies were A=0.3536, C=0.1276, G=0.1547 and T=0.3641, and rate matrix was 0.8753, 11.1191, 2.2551, 0.2431 and 15.2273.

The best- fit model of evolution selected for the nuclear data set was TrN+I. Base frequencies of A=0.2304, C=0.2741, G=0.2753 and T=0.2201, and rate matrix was 1.0000, 5.6155, 1.0000, 1.0000 and 9.7409 and an I value of 0.8169 for the ML analysis.

All of our MP, ML and Bayesian phylogenetic analyses based on mitochondrial genes revealed four well supported clades within the genus *Allogalathea* (Fig. 7). Topologies derived from MP, ML and BI were largely congruent although the internal nodes showed low statistical support. Our analysis suggests the existence of four deeply divergent clades, which may also be distinguished on the basis of subtle morphological differences. The monophyly of the genus was highly supported by all the tests (Fig. 7), though phylogenetic relationships were not fully resolved.

Allogalathea babai n. sp., *A. elegans* and *A. inermis* n. sp. always clustered together, but bootstrap and posterior probability support was low in all the tests (MP=77, ML=63 and BI=67). Phylogenetic relationships among these three species were not resolved and the tree topology reflected a trichotomy. In all tests, the species *A. longimana* n. sp. occupied a basal position.

The nuclear gene PEPCK was unable to resolve the phylogenetic relationships among the four clades. In each analysis, the monophyly of *A. babai* n. sp. and *A. inermis* n. sp. was supported. Despite a lack of resolution for defining the other two species, our Bayesian reconstruction indicated clear differentiation of the only specimen of *A. longimana* n. sp. examined from all specimens of *A. elegans*.

Discussion

Throughout 250 years of Linnaean taxonomy, species descriptions have mainly relied upon the study of morphological characters. Given the criteria used to define species could sometimes be controversial (Avise, 1994), the combined use of molecular and morphological data may help clarify species boundaries (Calvo *et al.*, 2009; Santos *et al.*, 2009). The incorporation of molecular tools into systematic studies have confirmed the taxonomic status of many taxa described on the basis of morphological data (Tautz *et al.*, 2003); however it has also unveiled a vast diversity hidden behind a great morphological similarity (Bickford *et al.*, 2007).

Cryptic speciation has been previously reported in the family Galatheidae (Machordom & Macpherson, 2004; Macpherson & Machordom, 2005). The present study provides further evidence of the important role played by this phenomenon in squat lobsters and confirms that the real diversity of the group is still far from being well-known (Baba *et al.*, 2008). The morphological differences detected here among the four *Allogalathea* species are very subtle, but constant in all the specimens examined. Our results reveal the taxonomic value of characters such those describing the spinulation and length of chelipeds (Fig. 6), spinulation of walking legs and shape of the rostrum. These subtle traits are useful to designate species to the genus *Allogalathea*, and could also probably be used in closely related genera (e.g. *Galathea*, *Allomunida*, *Sadayoshia* and *Lauriea*).

Phylogenetic reconstruction

Our phylogenetic reconstructions clearly indicate the existence of four strongly supported mitochondrial clades. Each of the clades recovered in this study are recognized as distinct species based on morphological and genomic features. The genus was identified as a monophyletic group, and although phylogenetic relationships were not fully resolved, the taxonomic status of the four species was highly supported by all the phylogenetic analyses.

The more conserved nuclear gene PECK was also unable to resolve phylogenetic relationships among the different groups, and only *A. babai* n. sp. and *A. inermis* n. sp. were recovered as monophyletic taxa. Thus, the PEPCK marker lacks the resolution needed to infer species-level relationships. This gene has been recently incorporated in the pool of nuclear protein coding genes used to infer relationships among high taxonomic levels of decapods (Tsang *et al.*, 2008; Ma, Chan & Chu, 2009). Tsang *et al.* (2008) reported a mean divergence of around 6% for PEPCK in three species of *Panulirus*, suggesting a good resolution power also for lower taxonomic ranks (e.g. genus or species).

The maximum divergence value observed here for PEPCK was around 4.5% and suggests insufficient variability for inferring phylogenetic relationships at the intrageneric level in galatheids. The use of this gene as a marker of relationships within and among different galatheid genera (e.g. *Paramunida* and *Agononida*) has also been tested and preliminary data indicate the same lack of

resolution observed here at species level but a better capacity to resolve intergeneric relationships (unpublished data).

Mitochondrial interspecific divergences within *Allogalathea* were clearly higher than those reported for species of other squat lobster genera, e.g. *Munida, Paramunida, Raymunida* (Machordom & Macpherson, 2004; Cabezas *et al.*, 2009). Lower mean mitochondrial divergences than those reported in the present study would be expected to return unresolved phylogenetic trees using the nuclear gene PECK as the marker. Resolution could perhaps be improved by combining this nuclear marker with non-coding ribosomal genes such as 18S rRNA or 28S rRNA.

The position ascribed by the mitochondrial genes to the single specimen from Christmas Islands (Allo8069) within the clade *A. babai* n. sp. is remarkable. This specimen was clearly differentiated in the phylogenetic tree from the rest of specimens of the clade (Fig. 7) and exhibited a mean divergence according to both mitochondrial genes of around 4.5%. Though similar divergences accompanied by the corresponding morphological data have been considered sufficient evidence to describe new species of other squat lobster genera (Macpherson and Machordom, 2001; Cabezas *et al.*, 2009), we were unable to detect any morphological difference to support the idea that this specimen belongs to a different species. Further, our amplification of the PEPCK gene failed in this specimen and we could not confirm its genetic differentiation at the nuclear level. Hence, until more specimens can be analyzed, we have designated specimen Allo8069 as *A. babai* n. sp.

Phylogeographic and evolutionary considerations

Macroecological studies have demonstrated that, in general, coastal species have smaller geographic ranges than species inhabiting the continental slope or abyssal plains (Macpherson, 2003). Until 20 years ago, species associated with deep marine strata were considered to have a wide distribution because these ecosystems were assumed to be homogenous and uniform (Wilson & Hessler, 1987).

Most species of the family Galatheidae are found in waters of the continental slope (200-2000 m) with the exception of *Allogalathea* and closely related genera (e.g. *Galathea*, Baba *et al.*, 2008), which live in shallow waters.

In general, galatheid species exhibit a moderately wide geographical range. However, numerous species of *Paramunida* and *Munida* are restricted to either a single or a few seamounts, islands or archipelagos (Samadi *et al.*, 2006; Cabezas, Macpherson & Machordom, 2009; Macpherson *et al.*, 2010; Rowden *et al.*, 2010). Although the main goal of this study was a taxonomic revision of the genus *Allogalathea*, some phylogeographic considerations can be inferred from our molecular data because the four species show different distributions. *Allogalathea elegans* shows an exceptionally wide distribution range across the Indo-Pacific Ocean, *A. babai* n. sp. and *A. inermis* n. sp. are both widely distributed in the West Pacific, and *A. longimana* n. sp. is the only with a distribution restricted to the Philippines (Fig. 7). Although these findings suggest no pattern within the geographic ranges of each species, specimens of *A. elegans* collected in Mozambique and Madagascar clustered separately in the phylogenetic tree, indicating that populations from the Indian Ocean are genetically different to those inhabiting the Pacific. However, more extensive sampling is needed to confirm either a pattern of isolation by distance, or a vicariant event that affected these two populations. In the case of the other two species, the differences observed among specimens from New Caledonia, Okinawa and Vanuatu (*A. babai* n. sp.) and among those from New Caledonia, Vanuatu and Thailand (*A. inermis* n. sp.) were discrete and no genetic structure was detected for the different regions.

Prior phylogeographic studies have shown effective barriers to genetic exchange between and within the Indian and Pacific Oceans (Williams & Benzie, 1997; Barber *et al.*, 2002; Crandall *et al.*, 2008). Nevertheless, our results suggest gene flow among *Allogalathea* specimens separated by thousands of kilometres, in agreement with other studies on coral reef fishes (Craig *et al.*, 2007; Horne *et al.*, 2008).

The use of molecular phylogenies to examine connectivity among marine populations can be very effective, but when the sample size is limited as in our investigation, any weak genetic population structure must be interpreted cautiously (Hedgecock, 2007). The apparent low genetic diversity revealed by our data could be explained by a great dispersal capability during the larval stage, yet ecological factors or historic events cannot be ruled out.

Any inferences concerning the dispersion of *Allogalathea* are highly speculative, since knowledge of larval development in Galatheidae is scarce (e.g. Guerao *et al.*, 2006). The diversification of the galatheid genus *Munida* has been dated as Middle or Late Miocene based on general mean divergence values for the 16S rRNA and COI genes (Machordom & Macpherson, 2004). The interspecific divergence found here for the COI gene ranged from 12% to 15%. Assuming a rough mean COI divergence of 1% to 2% per million years, diversification of the *Allogalathea* genus would have occurred during the Late Miocene. Although more accurate molecular calibrations are still necessary, this preliminary estimate is in agreement with datings proposed for other shallow water species distributed in the Indo-Pacific (McCafferty *et al.*, 2002; Williams & Duda, 2008). New data on the biology, phylogeny and ecology of these species as well as improved knowledge of the geological history of the Indo-Pacific region will help to clarify genetic connectivity among populations and the true diversity and evolutionary history of the genus.

Conclusions

The present findings illustrate the need to combine different sources of information when intraspecific variability in morphological characters is not clear. Our results highlight the importance of the subtle morphological differences mentioned by Baba for this group (1969, 1979). Characters describing the spinulation and length of chelipeds, spinulation of walking legs and shape of the rostrum can contribute greatly to the taxonomy of *Allogalathea*. The existence of more species of *Allogalathea* is likely and a more detailed study designed to fill in distribution range gaps, including more specimens is recommended.

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Figure legends

Figure 1. *Allogalathea babai* n. sp., holotype (ovig. F 5.4 mm, New Caledonia (Lagoon, 8 September 1993). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right P1, dorsal. F, right P2, lateral. G, right P3, lateral. H, right P4, lateral. Scales: A, E-H = 1 mm; B-D = 2 mm.

Figure 2. *Allogalathea elegans* (Adams & White, 1848), (ovig. F 5.6 mm, New Caledonia, Touho Bank, 28 August 1993). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right P1, dorsal. F, right P2, lateral. G, right P3, lateral. H, right P4, lateral. Scales: A, E-H = 1 mm; B-D = 2 mm.

Figure 3. *Allogalathea elegans* (Adams & White, 1848), lectotype (F 5.0 mm, Philippines, Corregidor). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing right antennule and antenna, ventral D, right Mxp3, lateral. E, right detached P1, dorsal. F, left detached P1. G, right detached P3. H, left detached P4. Scales: A, B-D, G, H = 1 mm; E, F = 0.5 mm. The detached pereiopods could belong to the paralectotype (M 4.1 mm).

Figure 4. *Allogalathea inermis* n. sp., holotype (ovig. F 7.3 mm, New Caledonia, SMIB 5, Stn DW100). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right P1, dorsal. F, right P2, lateral. G, right P3, lateral. H, left P4, lateral. Scales: A, E-H = 1 mm; B-D = 2 mm.

Figure 5. *Allogalathea longimana* n. sp., holotype (ovig. F 6.5 mm, Philippines, MUSORSTOM 3, Stn CP107). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right P1 palm and fingers, dorsal. F, right P1 merus and carpus, dorsal. G, right P3, lateral. H, right P4, lateral. Scales: A, E-H = 1 mm; B-D = 2 mm.

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Table legends

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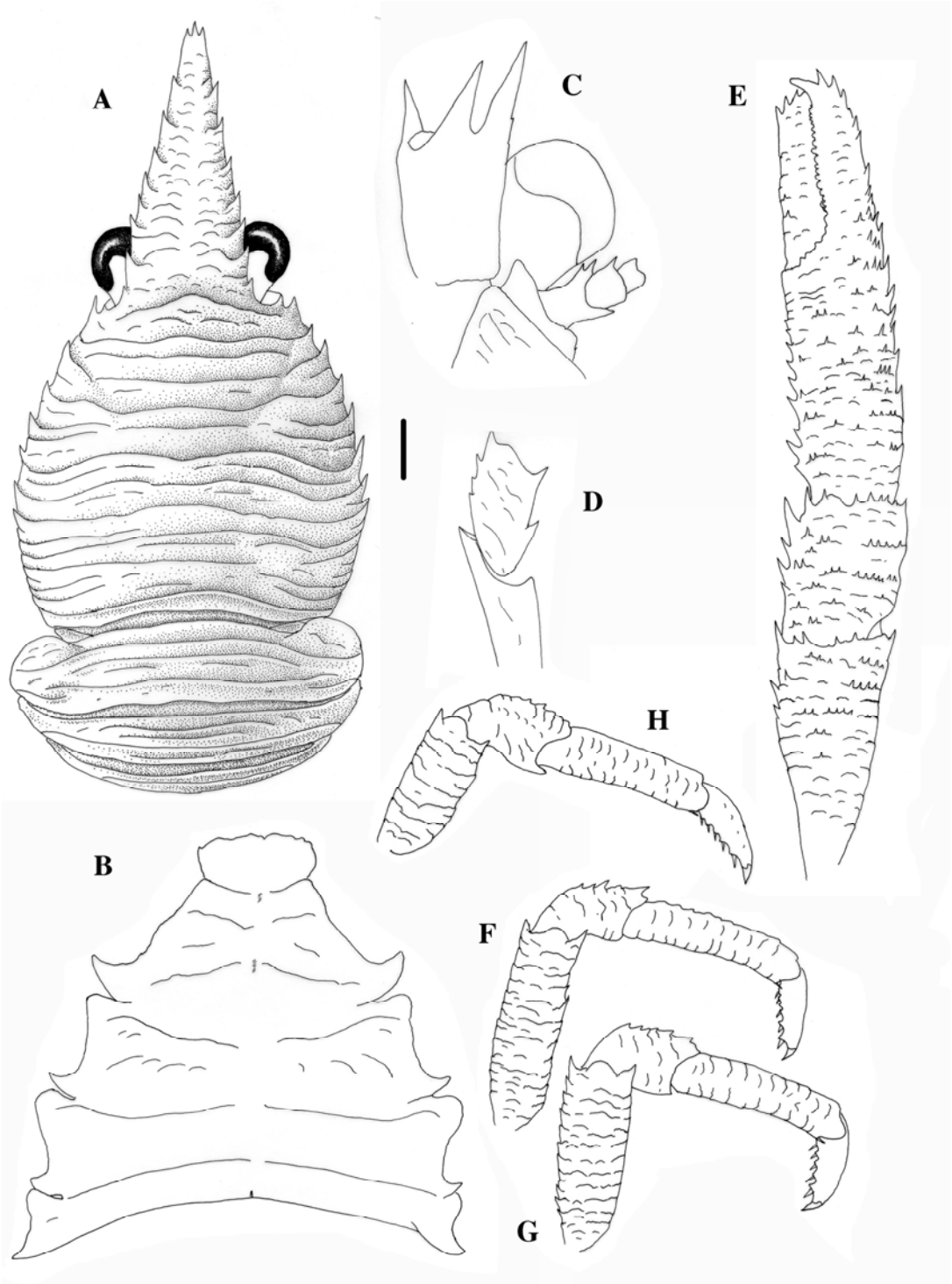
Appendix

Dorsal view. A. *Allogalathea babai* n. sp. , SANTO, Stn FR1-CF1, ovigerous female 8.4 mm; B. *A. elegans* (Adams & White, 1848), SANTO, Stn FR1-CF2, male 4.1 mm; C, *A. elegans* (Adams & White, 1848), SANTO, Stn AT81, ovigerous female 6.0 mm; D, *A. inermis* n. sp., SANTO, Stn NR8, male 3.1 mm.



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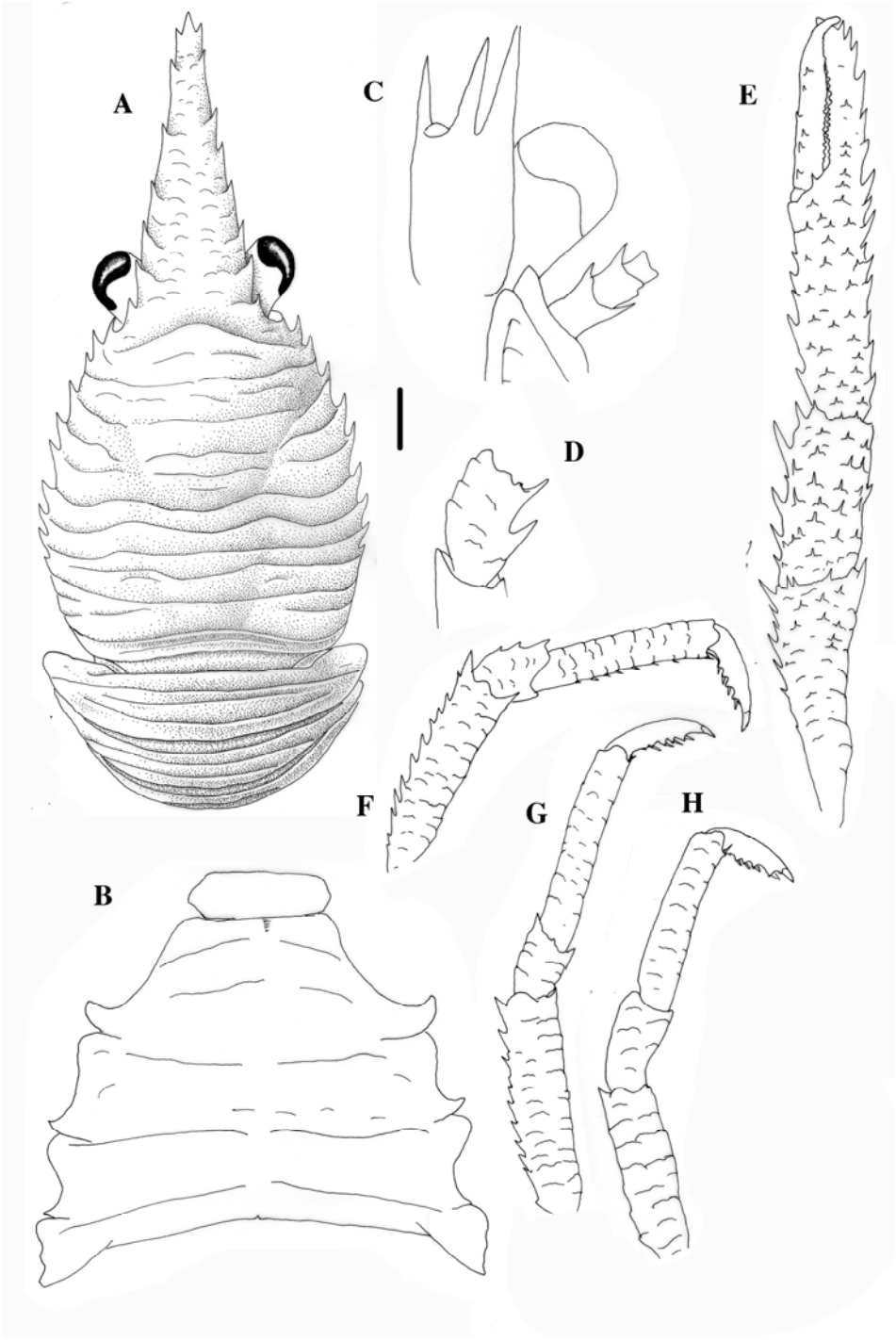

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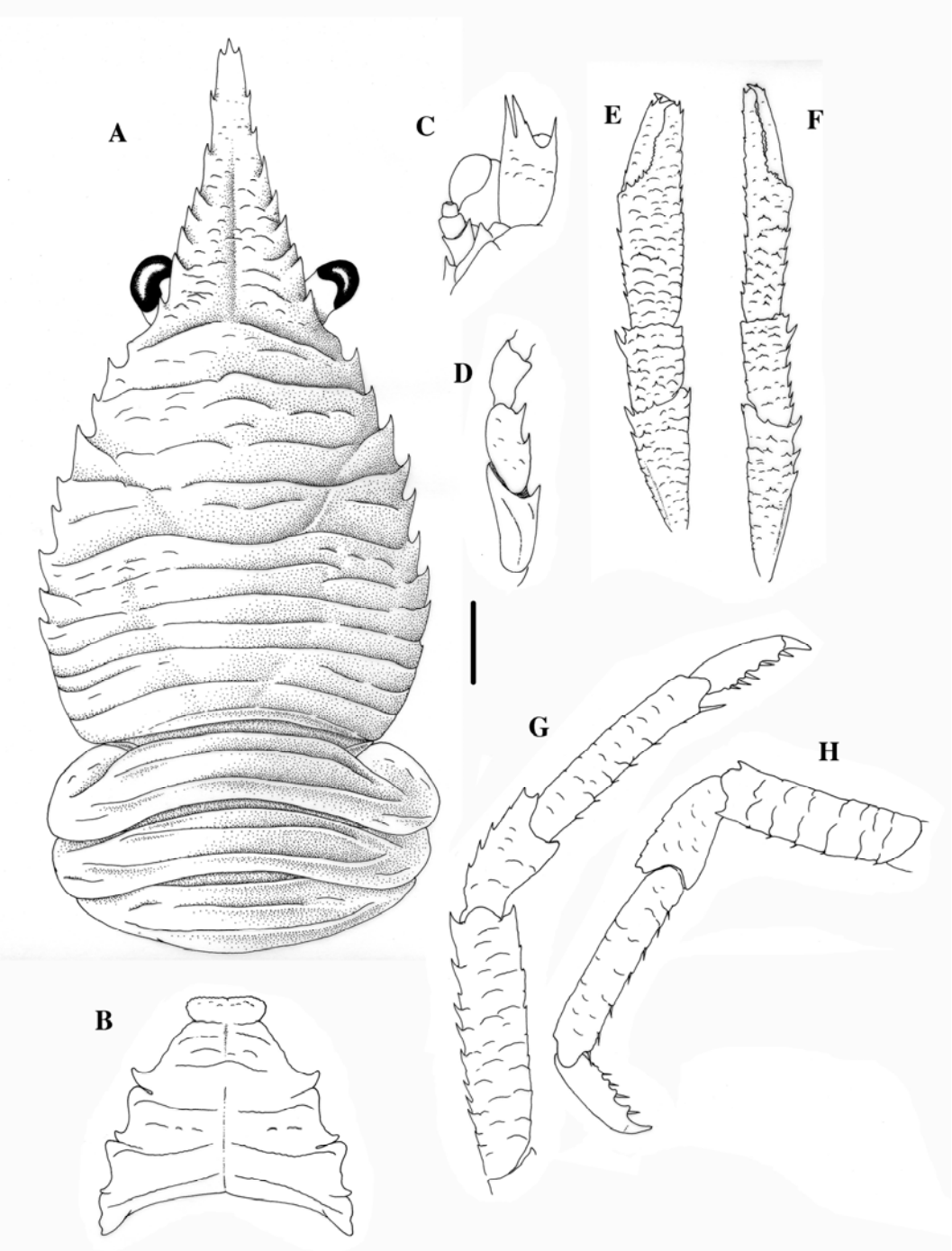
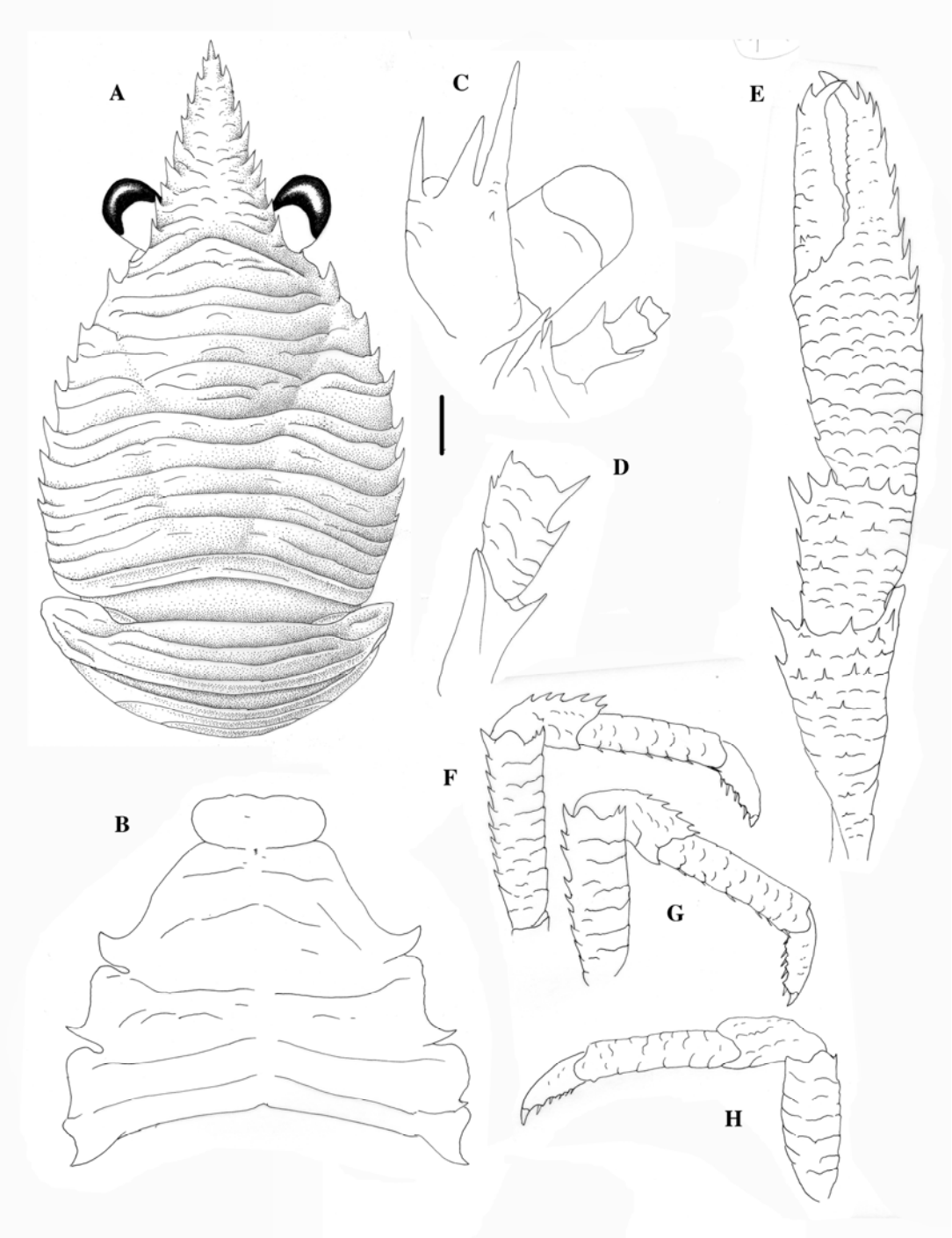


Figure 3. *Allogalathea elegans* (Adams & White, 1848), syntype (F 5.0 mm, Philippines, Corregidor). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing right antennule and antenna, ventral D, right Mxp3, lateral. E, right detached P1, dorsal. F, left detached P1. G, right detached P3. H, left detached P4. Scales: A, B-D, G, H = 1 mm; E, F = 0.5 mm. The detached pereiopods could belong to the second syntype (M 4.1 mm).



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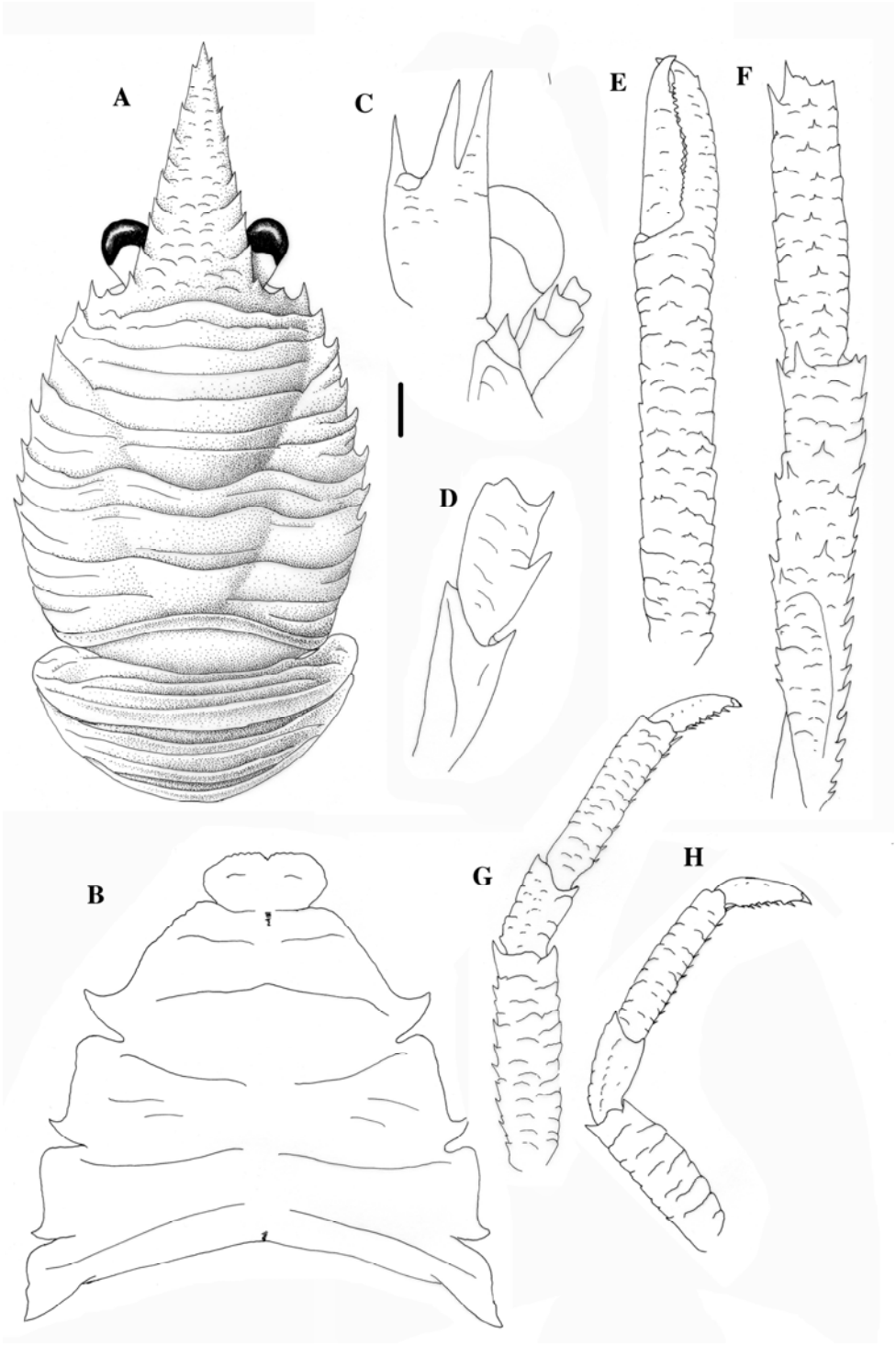
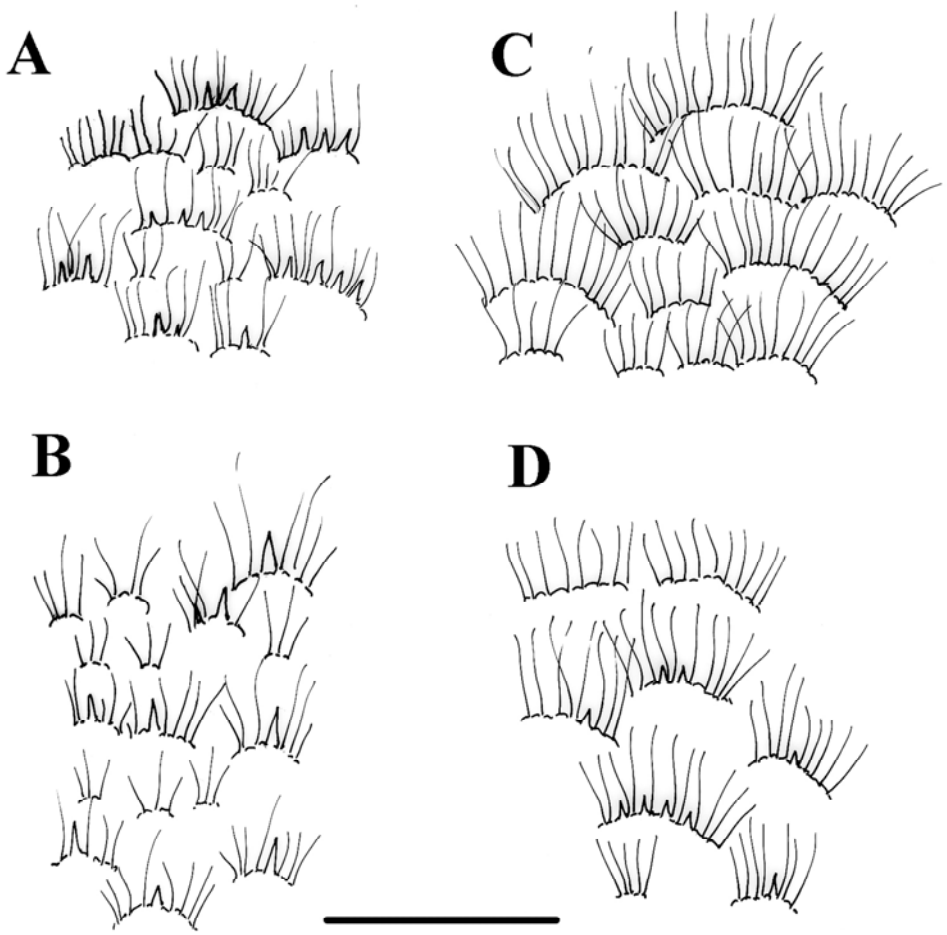


Figure 5. *Allogalathea longimana* n. sp., holotype (ovig. F 6.5 mm, Philippines, MUSORSTOM 3, Stn CP107). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right P1 palm and fingers, dorsal. F, right P1 merus and carpus, dorsal. G, right P3, lateral. H, right P4, lateral. Scales: A, E-H = 1 mm; B-D = 2 mm.



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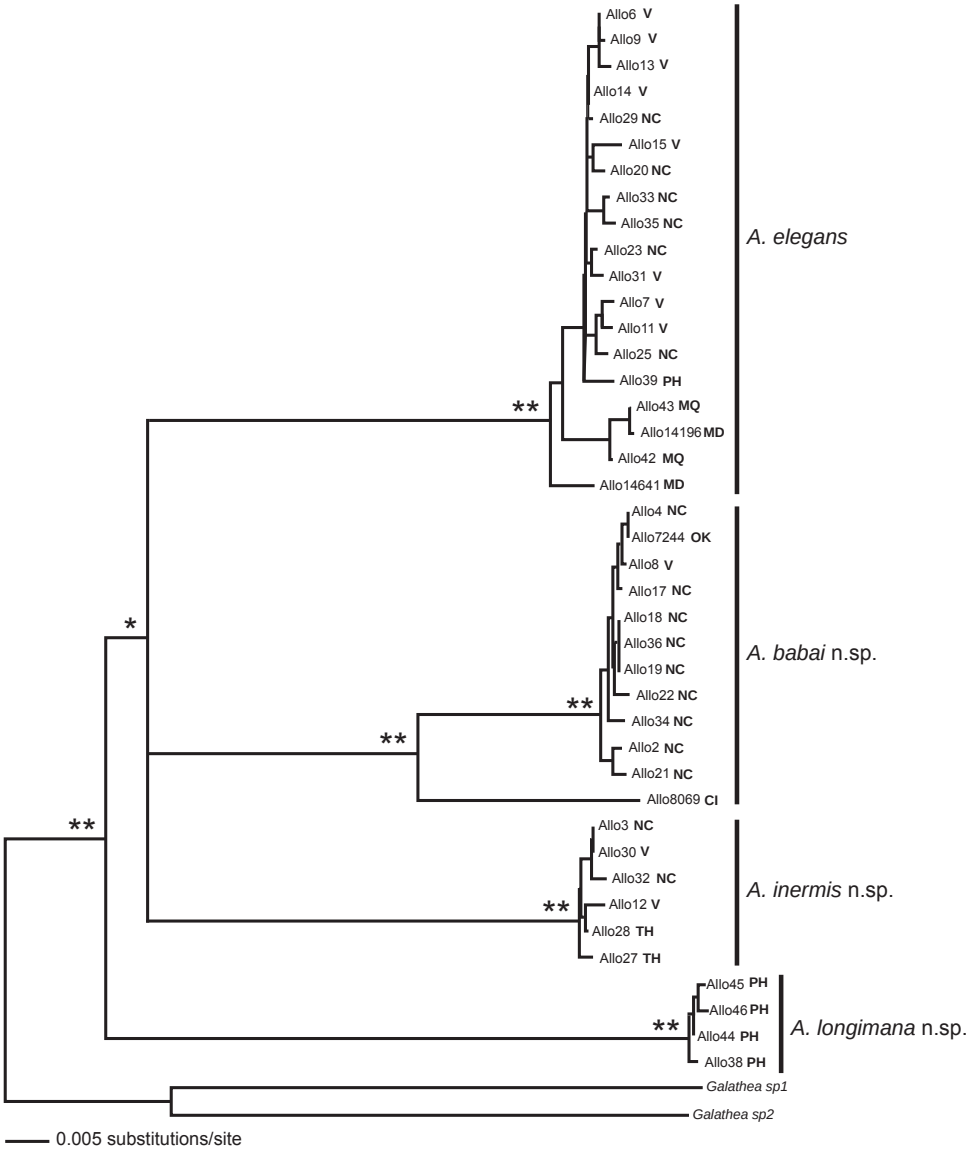

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Species	Code	Locality	Depth (m)	Cruise	16S rRNA	COI	PEPCK
A. babai n.sp.	Allo2	New Caledonia	15-35	LIFOU	GU392121	GU392164	X
A. inermis n.sp.	Allo3	New Caledonia	120	SMIB 5	GU392122	GU392165	X
A. babai n.sp.	Allo4	New Caledonia	15-35	LIFOU	GU392123	GU392166	GU392207
Galathea sp1	Allo5	New Caledonia	15-20	LIFOU	GU392124	GU392167	GU392208
A. elegans	Allo6	Vanuatu	58-59	SANTO	GU392125	GU392168	GU392209
A. elegans	Allo7	Vanuatu	46-55	SANTO	GU392126	GU392169	GU392210
A. babai n.sp.	Allo8	Vanuatu	18-20	SANTO	GU392127	GU392170	GU392211
A. elegans	Allo9	Vanuatu	Intertidal	LIFOU	GU392128	GU392171	GU392212
Galathea sp2	Allo10	New Caledonia	Intertidal	LIFOU	GU392129	GU392172	GU392213
A. elegans	Allo11	Vanuatu	18-20	SANTO	GU392130	GU392173	X
A. inermis n.sp.	Allo12	Vanuatu	11	SANTO	GU392131	GU392174	GU392214
A. elegans	Allo13	Vanuatu	86-118	SANTO	GU392132	GU392175	GU392215
A. elegans	Allo14	Vanuatu	71-104	SANTO	GU392133	GU392176	X
A. elegans	Allo15	Vanuatu	0-45	SANTO	GU392134	GU392177	GU392216
A. babai n.sp.	Allo17	New Caledonia	No depth	Lagoon Samples	GU392135	GU392178	X
A. babai n.sp.	Allo18	New Caledonia	No depth	Lagoon Samples	GU392136	GU392179	GU392217
A. babai n.sp.	Allo19	New Caledonia	No depth	Lagoon Samples	GU392137	GU392180	GU392218
A. elegans	Allo20	New Caledonia	No depth	Lagoon Samples	GU392138	GU392181	GU392219
A. babai n.sp.	Allo21	New Caledonia	No depth	Lagoon Samples	GU392139	GU392182	GU392220
A. babai n.sp.	Allo22	New Caledonia	No depth	Lagoon Samples	GU392140	GU392183	X
A. elegans	Allo23	New Caledonia	No depth	Lagoon Samples	GU392141	GU392184	GU392221
A. elegans	Allo25	New Caledonia	No depth	Lagoon Samples	GU392142	GU392185	GU392222
A. inermis n.sp.	Allo27	Thailandia	No depth		GU392143	GU392186	X
A. inermis n.sp.	Allo28	Thailandia	No depth		GU392144	GU392187	X
A. elegans	Allo29	New Caledonia	56	Lagoon Samples	GU392145	GU392188	X
A. inermis n.sp.	Allo30	Vanuatu	11	SANTO	GU392146	GU392189	X
A. elegans	Allo31	Vanuatu	102-120	SANTO	GU392147	GU392190	GU392223
A. inermis n.sp.	Allo32	New Caledonia	No depth	Lagoon Samples	GU392148	GU392191	GU392224
A. elegans	Allo33	New Caledonia	No depth	Lagoon Samples	GU392149	GU392192	GU392225
A. babai n.sp.	Allo34	New Caledonia	No depth	Lagoon Samples	GU392150	GU392193	GU392226
A. elegans	Allo35	New Caledonia	No depth	Lagoon Samples	GU392151	GU392194	GU392227
A. babai n.sp.	Allo36	New Caledonia	No depth	Lagoon Samples	GU392152	GU392195	GU392228
A. longimana n.sp.	Allo38	PhilippInes	111-115	MUSORSTOM 3	GU392153	GU392196	GU392229
A. elegans	Allo39	PhilippInes	73-84	MUSORSTOM 3	GU392154	GU392197	X
A. elegans	Allo42	Mozambique	100-110	MAINBAZA	GU392155	GU392198	GU392230
A. elegans	Allo43	Madagascar	26		GU392156	GU392199	X
A. longimana n.sp.	Allo44	PhilippInes	189-194	MUSORSTOM 3	GU392157	GU392200	X
A. longimana n.sp.	Allo45	PhilippInes	120-123	MUSORSTOM 3	GU392158	GU392201	X
A. longimana n.sp.	Allo46	PhilippInes	111-115	MUSORSTOM 3	GU392159	GU392202	X
A. elegans	Allo14196	Madagascar	0-12		GU392160	GU392203	GU392231
A. elegans	Allo14641	Madagascar	24-25		GU392161	GU392204	GU392232
A. babai n.sp.	Allo7244	Okinawa	18-23		GU392162	GU392205	X
A. babai n.sp.	Allo8069	Christmas Islands	No depth		GU392163	GU392206	GU392233

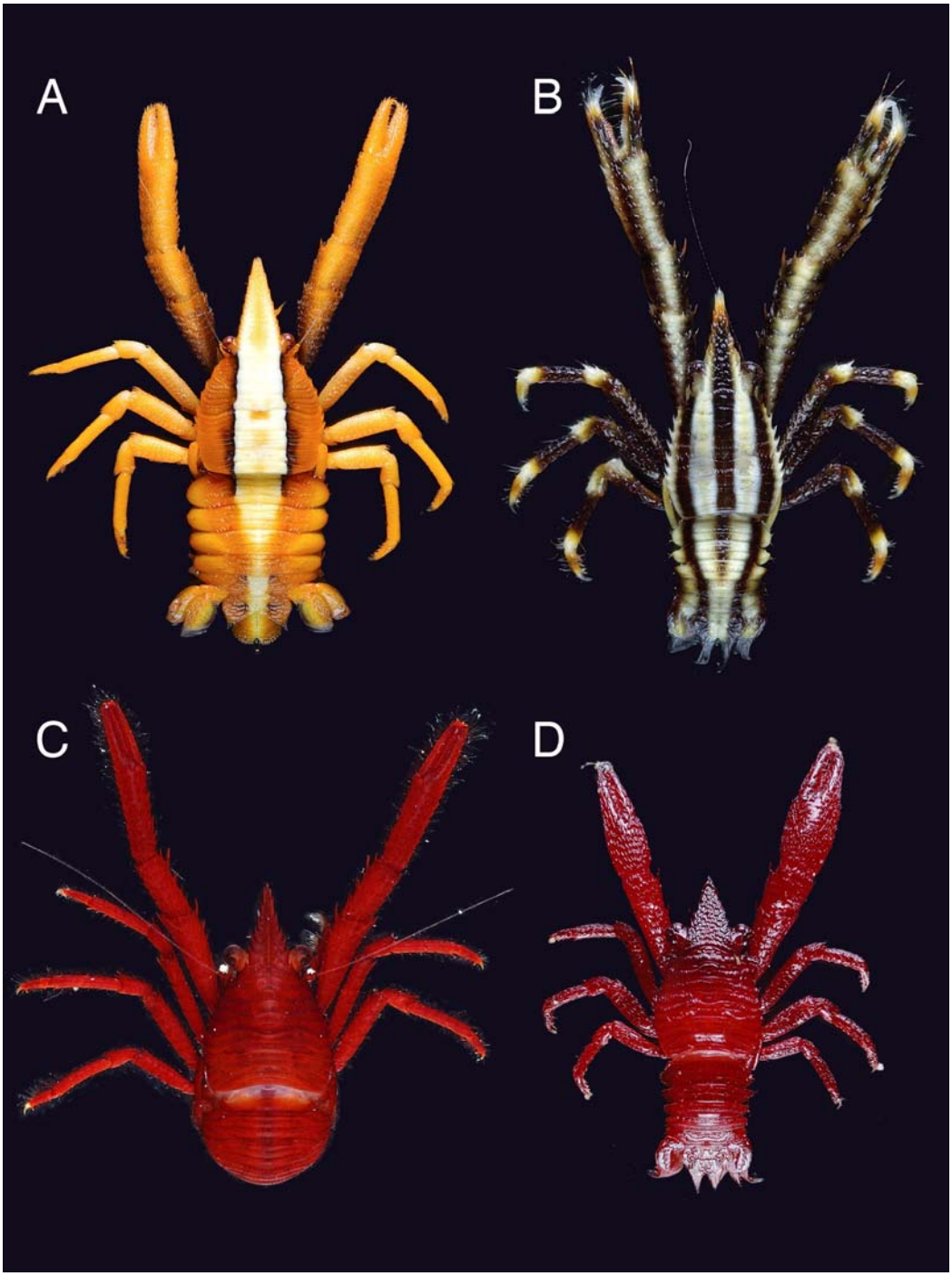
Table 1. Species of *Allogalathea* examined genetically and their corresponding codes in the phylogenetic tree, geographic location, depth, cruise, and GenBank Accession number.

Target gene	Primer	Direction	Primer sequence	Reference
16S rRNA	16S-F2	Forward	CGRGYTTTTATATCTGGTT	Present study
	16S-R	Reverse	TTATGCTACCTTRGCACAG	Present study
	16S-AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi et al., 1991
	16S-BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi et al., 1991
COI	LCO-1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994
	COI-H	Reverse	TCAGGGTGACCAAAAAATCA	Machordom and Macpherson, 2004
PEPCK	PEPCK-for2	Forward	GCAAGACCAACCTGGCCATGATGAC	Tsang et al., 2008
	PEPCK-rev3	Reverse	CGGGYCTCCATGCTSAGCCARTG	Tsang et al., 2008

Table 2. Primer sequences used for PCR amplification.

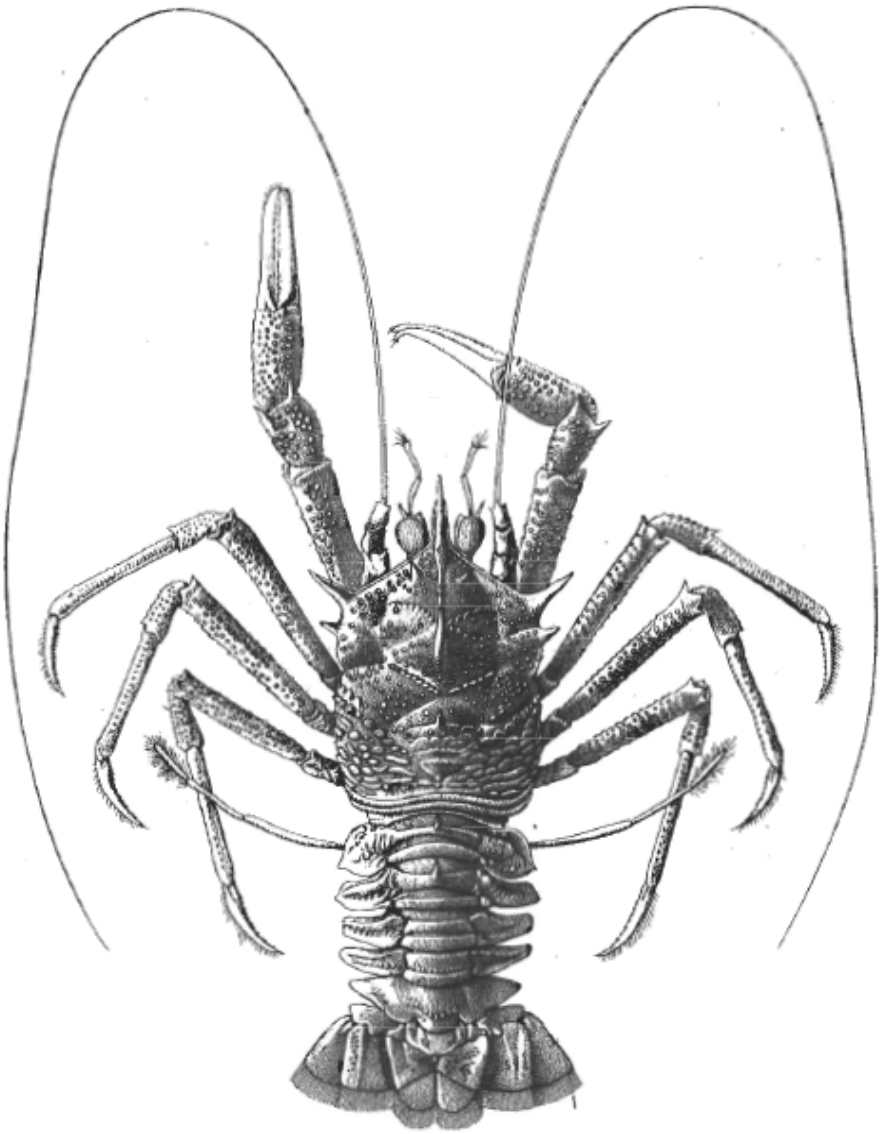
	A. elegans	*A. babai* n.sp.	*A. inermis* n.sp.	*A. longimana* n.sp.
A. elegans	**X**	8.70-9.43%	8.40-9.22%	10.33-11.02%
***A. babai* n.sp.**	12.31-13.56%	**X**	8.70-9.99%	10.28-11.08%
***A. inermis* n.sp.**	12.15-13.52%	10.94-12.31%	**X**	11.33-12.06%
***A. longimana* n.sp.**	14.43-15.53%	12.86-13.67%	14.43-15.04%	**X**

Table 3. Mitochondrial pairwise distance values among *Allogalathea* species. Distances above the diagonal refer to the 16S rRNA gene and below the diagonal to the COI gene.



Appendix

Dorsal view. A. *Allogalathea babai* n.sp. , SANTO, Stn FR1-CF1, ovigerous female 8.4 mm; B. *A. elegans* (Adams & White, 1848), SANTO, Stn FR1-CF2, male 4.1 mm; C, *A. elegans* (Adams & White, 1848), SANTO, Stn AT81, ovigerous female 6.0 mm; D, *A. inermis* n.sp., SANTO, Stn NR8, male 3.1 mm.



Galacantha diomedeae Faxon, 1893

CAPÍTULO IV

Taxonomic revision of the genus *Paramunida* Baba, 1988 (Crustacea: Decapoda: Galatheidae): a morphological and molecular approach.

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[2]*Centro de Estudios Avanzados de Blanes (CSIC). Carr. Acc. Cala Sant Francesc 14. 17300 Blanes. Girona. Spain.* [2]*macpherson@ceab.csic.es*

Key words: New species, squat lobster, morphology, molecular data, Galatheidae, *Paramunida*

Abstract
The genus *Paramunida* belongs to the family Galatheidae, one of the most diverse families among anomuran decapod crustaceans. Despite of the genus has received a great taxonomic attention; subtle morphological variations observed in numerous samples suggest the existence of undescribed species. The revision of many specimens collected during recent expeditions and the morphological and molecular comparison with the previously described species have revelaled the existence of eleven new lineages. All of them are identified by subtle and constant morphological differences, which are in agreement with molecular divergences reported for the mitochondrial markers ND1 and 16S rRNA. Here, we describe and illustrate the new species, providing a briefly redescription for the previously known species and a diagnostic identification key.

Introduction
The galatheid crabs of the genus *Paramunida* Baba, 1988 are distributed across the Indian and Pacific Oceans and are commonly found living on the continental shelf and slope between 200 and 500 m (Baba *et al.*, 2008; Macpherson *et al.*, 2010). The genus was established in 1988 by Baba to include some species previously adscribed to the genus *Munida.* The species are characterized by having a short rostrum, reduced transverse ridges and striae on the carapace, the antennal peduncle with a well-developed anterior prolongation of segment 1 and the male gonopods absent from the first abdominal somite. Subsequent, a phylogenetic study including numerous species of the genus showed that the group is monophyletic (Machordom & Macpherson, 2004).
Thus, Baba (1988) included 7 species: *P. granulata* (Henderson, 1885), *P. hawaiiensis* (Baba, 1981), *P. longior* Baba, 1988, *P. proxima* (Henderson, 1885), *P. scabra* (Henderson, 1885), *P. setigera* Baba, 1988 and *P. tricarinata* (Alcock, 1894). The taxonomy of the genus received a remarkable improvement after the large sampling effort carried out in waters around the Philippines, Indonesia and New Caledonia (Macpherson, 1993; Baba, 2005), Wallis and Futuna (Macpherson, 1996), East Australia (Ahyong & Poore, 2004), Fiji and Tonga (Macpherson, 2004), French Polynesia (Macpherson, 2006), New Zealand (Ahyong, 2007), Taiwan and Japan (Baba *et al.*, 2009; Macpherson & Baba, 2009), and Solomon Islands (Cabezas *et al.*, 2009). At present 26 species are known (Baba *et al.*, 2008, 2009; Cabezas *et al.*, 2009) and although the status of most of them is clear, the variability of several morphological characters (e.g. length and shape of antennal spines) suggests the existence of cryptic species (Macpherson, 2006). Previous works have shown the existence of cryptic species within the family Galatheidae (e.g. *Agononida*, *Allogalathea*, *Babamunida*, *Munida* (Macpherson & Machordom, 2005; Macpherson & Baba, 2009; Schnabel *et al.*, 2009; Cabezas *et al.*, 2010)), hence a revision of the morphological and molecular differences

of the species of *Paramunida* is strongly recommended.
In the present revision, the study of numerous representatives of *Paramunida* obtained during recent expeditions to Vanuatu, New Caledonia, Chesterfield Islands, Philippines and SW Indian Ocean has revealed the existence of additional species. Here, we describe and illustrate 11 new species of *Paramunida* and provide a diagnosis of the previously known species of the genus. The most important morphological characters are emphasized in combination with molecular data from two mitochondrial markers (16S rRNA and ND1) to support the taxonomic status of each species.

Material and methods

Sampling and identification
Specimens were collected using beam trawls or Waren dredges in expeditions to SW Indian Ocean in 1976 and 2009 (MD08, MAINBAZA), Chesterfield Islands in 2005 (EBISCO), Philippines in 2005 (PANGLAO), and Vanuatu in 2006 (SANTO). We also used the type material and topotypic specimens of each species deposited in the Muséum national d'Histoire naturelle, Paris (MNHN). Unfortunately, the types of several species have not been studied (e.g. *P. tricarinata*) since we could not access to the material. The size of the carapace is indicated as the postorbital carapace length measured along the dorsal midline from the posterior margin of the orbital to the posterior margin of the carapace. The terminology used mainly follows Baba *et al.* (2009). The abbreviations used are: Mxp3 = third maxilliped, P1 = first pereopod (cheliped), P2–4 = second to fourth pereopods (first to third walking legs). The length of the antennular and antennal segments are always measured excluding distal spines, and along their lateral margins; the width is measured at midlength of each segment. All specimens, including the types of the new species are deposited in the Museum national d'Histoire naturelle, Paris (MNHN), and the collection of the National Taiwan Ocean University (NTOU).

Molecular analyses
Total genomic DNA was isolated from muscle tissue or pereopods using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen). Two mitochondrial markers were amplified (16S rRNA and ND1). Amplification reactions were performed in a final volume of 50 µl, the PCR mix contained 2 µl of DNA template, 0.16 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer (containing a final concentration of 2 mM $MgCl_2$), 0.5 µl of BSA (10 mg/ml), 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. The partial 16S rRNA was amplified using the new forward designed primer 16S rRNAF3 5′-AAA GGC CGC GGT ATA TTA A-3′ and the reverse primer 16S rRNAbr-H from Palumbi (1991). For the ND1, the primers ND1 af-P and ND1ar-P from Pérez-Barros *et al.* (2008) were used. Thermal cycling conditions consisted of an initial denaturation step of 94ºC for 4 min followed by 39 cycles at 94ºC for 30 s, an annealing temperature of 45.5ºC (16S rRNA) and 40.5º (ND1) for 1 min, 72ºC for 1 min, and a final extension at 72ºC for 10 min. Samples were cycle-sequenced using the ABI Prism BigDye Terminator, and subsequently were run on an ABI 3730 Genetic Analyzer (Applied Biosystems, ABI). Sequences for the 16S rRNA from previous works were used (Machordom & Macpherson, 2004; Cabezas *et al.*, 2009). New sequences are available in GenBank under accession numbers GU814955-GU815088 and HM173357-HM173530.

Results
The eleven new species can be identified on the basis of subtle and constant morphological differences, which match clear differences in molecular sequences from the markers 16S rRNA and ND1. The divergences between each pair of taxa ranged from 1.18% to 13.94% for

the 16S rRNA and from 2.06% to 20.66% for the ND1 (Table 1).
Material from the species *P. spatula* and *P. antipodes* could not be molecularly examined, and the species *P. hawaiiensis* and *P. marionis* failed the amplification since material was preserved in formaline. The taxonomic status of the specimens named as *P. aff. longior* and *P. aff. setigera* (see under Material examined of *P. longior* and *P. tenera*, respectively) could not be assessed with confidence because they were so damaged that morphological characters were hardly visible. Although molecular divergence values suggest that they could represent new lineages, we do not take any formal decision until more specimens can be analyzed.

Systematic account

Genus *Paramunida* Baba, 1988

Paramunida Baba, 1988: 175 (gender: feminine). — Poore, 2004: 239. — Baba, 2005: 197. — Baba *et al.*, 2008: 171 (compilation of species). — Baba *et al.*, 2009: 277.

Type species: *Paramunida setigera* Baba, 1988, by original designation.

DIAGNOSIS. — (from Baba *et al.*, 2009) Carapace covered with spinules or granules, transverse striae indistinct. Rostrum short, basally subtriangular, distally ending in spine. Supraocular spines short and stout, usually remote from rostral spine. Abdominal somites with 2 main transverse ridges, each with spines in regular arrangement. Basal segment of antennule with distomesial and distolateral spines, both small; lateral spines obsolescent. Antennal peduncle with strong anterior prolongation on segment 1, flagellum of no great length. P1–4 squamous; P2–4 propodi successively longer posteriorly; dactyli slender, curved and somewhat twisted, with flexor margin entire. G1 absent in males.

REMARKS. — Until the present study, the genus comprised 26 species distributed across the Indo West Pacific (Baba *et al.*, 2008; Cabezas *et al.*, 2009; Macpherson & Baba, 2009). Most species are distributed in the western part, two of which also occurs in the Indian Ocean (*P. scabra, P. tricarinata*) and with 3 species occurring in the Central Pacific (*P. hawaiiensis, P. pictura, P. spatula*). In general they exhibit a distribution highly restricted to single islands or archipielagos, with a few species widely distributed (see Baba *et al.*, 2008). Bathymetrically, the genus is typically recorded in transitional depths (200-500 m), with few of them distributed in the continental shelf or in the upper bathyal depths (Baba, 2005). The present paper adds 11 new species to the genus.

Key to species of the genus *Paramunida*

1 Anterior prolongation of antennal segment 1 spatulate ..... *P. spatula* Macpherson, 2006
- Anterior prolongation of antennal segment 1 spiniform 2

2 Rostral spine smaller or at most equal than supraocular spines 3
- Rostral spine larger than supraocular spines 7

3 Margin between rostral and supraocular spines convex ..... *P. curvata* Macpherson, 2004
- Margin between rostral and supraocular spines straight or slightly concave 4

4 Antennal segment 2 with minute distomesial spine..... *P. microrhina* n.sp.
- Antennal segment 2 with well developed distomesial spine 5

5 Mesogastric region with 3 well developed spines. Bundle of setae at base of carpus of P1 absent ..... *P. hawaiiensis* (Baba, 1981)
- Mesogastric region with minute spines. Bundle of setae at base of carpus of P1 present or absent 6

6 Sternal plastron with numerous striae. Bundle of setae at base of carpus of P1 present .... *P. setigera* Baba, 1988
- Sternal plastron with few striae, sternites 5–7 with few striae on each side. Bundle of setae at base of carpus of P1 absent ..... *P. tenera* n. sp.

7 Distomesial spine of antennal segment 2 almost reaching end of anterior prolongation of segment 1 ..... *P. granulata* (Henderson, 1885)
- Distomesial spine of antennal segment 2 far falling short of end of anterior prolongation of segment 1 8

8 P2–4 propodi slender, about 20 times as long as broad ..... *P. longior* Baba, 1988
- P2–4 propodi 7–14 times as long as broad 9

9 Distomesial spine of antennal segment 2 mucronated or blunty produced 10
- Distomesial spine of antennal segment 2 spiniform..... 22

10 Mesogastric region with 1 (rarely 2) spine 11
- Mesogastric region with a row of 3–4 distinct spines 13

11 Sternal plastron with numerous striae..... *P. proxima* (Henderson, 1885)
- Sternal plastron with few striae, sternites 5–7 with few striae on each side 12

12 Distomesial spine of antennal segment 2 clearly overreaching antennal peduncle..... .. .. *P. belone* Macpherson, 1993
- Distomesial spine of antennal segment 2 nearly reaching end of antennal peduncle ....*P. antipodes* Ahyong & Poore, 2004

13 Distomesial spine of antennal segment 2 slightly or clearly overreaching antennal peduncle..... 14
- Distomesial spine of antennal segment 2 clearly not reaching end of antennal peduncle ...

..... 19

14 Lateral margin of antennular segment 1 with convex (proximal) portion as long as straight (distal) portion ..... *P. spica* n. sp.
- Lateral margin of antennular segment 1 with convex (proximal) portion clearly longer than straight (distal) portion..... 15

15 Distolateral spine of antennal segment 2 exceeding antennal segment 3 ....*P. salai* Cabezas *et al.*, 2009
- Distolateral spine of antennal segment 2 not reaching end of antennal segment 3 16

16 Mesial margin of antennal article 2, including distal spine, straight. Rostrum triangular or spiniform 17

- Mesial margin of antennal article 2, including distal spine, convex. Rostrum spiniform.... 18

17 Rostral spine triangular. ..... *P. ascella* n. sp.
- Rostral spine spiniform. ..... *P. mozambica* n. sp.

18 Distomesial spine of antennal segment 2 shorter than rest of segment 2. Gastric region with short striae. Antennal segment 3 about 1.5 times longer than broad..... .....*P. stichas* Macpherson, 1993
- Distomesial spine of antennal segment 2 as long as rest of segment 2. Gastric region with moderate-sized striae. Antennal segment 3 about twice longer than broad .... *P. lophia* Cabezas *et al.*, 2009
19 Mesogastric region without well-developed spines ..... *P. parvispina* n. sp.
- Mesogastric region with a row of 3–4 distinct spines 20

20 Sternal plastron with numerous striae. Segment 2 of antennal peduncle bluntly produced distomesially ..... *P. evexa* Macpherson, 1993
- Sternal plastron with few striae, sternites 5–7 with few striae on each side. Segment 2 of antennal peduncle produced distomesially ending in distinct spine 21

21 Rostrum triangular. Propodus of walking legs more than 1.5 times dactylus length .... *P. echinata* Macpherson, 1999
- Rostrum spiniform. Propodus of walking legs slightly longer than dactylus .... *P. labis* Macpherson, 1996

22 Rostrum with thick dorsal carina ..... *P. cristata* Macpherson, 2004
- Rostrum with thin dorsal carina 23

23 Distomesial spine of antennal segment 2 clearly exceeding antennal peduncle ....*P. leptotes* Macpherson & Baba, 2009
- Distomesial spine of antennal segment 2 not reaching or at most slightly exceeding antennal peduncle 24

24 Mesogastric region with 1 (rarely 2) spine 25
- Mesogastric region with a row of 3–4 distinct spines 28

25 Median cardiac region with 1 spine ..... *P. pronoe* Macpherson, 1993
- Median cardiac region with a row of 3–4 spines 26

26 Tuffs of long and dense setae along anterior branch of cervical groove .....
..... *P. crinita* n. sp.
- Few and short setae along anterior branch of cervical groove 27

27 Sternal plastron with few striae, sternites 5–7 only with few striae on each lateral side .
.....*P. polita* Macpherson, 1993
- Sternal plastron with numerous striae ..... *P. scabra* (Henderson, 1885)

28 Sternal plastron with numerous striae…….... 29
- Sternal plastron with few striae, sternites 5–7 only with few striae on each lateral side…… 30

29 Antennal segment 3 twice as long as broad. Few and short setae along anterior branch of cervical groove ..... *P. thalie* Macpherson, 1993
- Antennal segment 3 slightly longer than broad. Tuffs of long and dense setae along anterior branch of cervical groove..... *P. tricarinata* (Alcock, 1894)

30 Distomesial spine of antennal segment 2 reaching or overreaching end of antennal peduncle. Distolateral spine of antennal segment 2 reaching or slightly exceeding end of antennal segment 3 ..... *P. marionis* n. sp.
.....
- Distomesial spine of antennal segment 2 not reaching end of antennal peduncle. Distolateral spine of antennal segment 2 not reaching end of antennal segment 3 31

31 Antennal segment 3 more than twice longer than broad .... .. *P. amphitrita* Macpherson, 1996
- Antennal segment 3 as long as broad 32

32 Antennal segment 2 as long as or more than 3 times longer than broad 33
- Antennal segment 2 at most twice longer than broad..... 34

33 Distomesial spine of antennal segment 2 reaching or slightly overreaching end of antennal segment 3 ..... *P. pictura* Macpherson, 1993
- Distomesial spine of antennal segment 2 not reaching end of antennal segment 3 .....
.....*P. poorei* n. sp.
34 Antennal segment 2 slightly longer than broad .....
..... *P. cretata* Macpherson, 1996
- Antennal segment 2 twice longer than broad 35

35 Row of small epigastric spines behind rostral spine absent .....
..... *P. luminata* Macpherson, 1996
- Row of small epigastric spines behind rostral spine present 36

36 P2–4 propodi less than 10 times longer than high. Merocarpal articulation of P3 clearly exceeding end of anterior prolongation of antennal segment 1 ..... *P. antares* n. sp.
- P2–4 propodi more than 10 times longer than high. Merocarpal articulation of P3 slightly exceeding end of anterior prolongation of antennal segment 1..... *P. achernar* n. sp.

Paramunida achernar n.sp.
Figs. 1, 12A

Paramunida cretata Macpherson, 2004: 283 (not *P. cretata* Macpherson, 1996)

TYPE MATERIAL. — *Holotype*: Tonga. BORDAU 2. Stn CP1643, 21°04.54'S, 175°22.50'W, 22 June 2000, 487 m: 1 ov. F 9.6 mm (MNHN-Ga xxxx).

Paratypes: Tonga. BORDAU 2. Stn CP1510, 21°04.65'S, 175°22.52'W, 31 May 2000, 461-497 m: 2 M 9.3-9.7 mm, 1 F 9.2 mm (MNHN-Ga xxx).

ETYMOLOGY. — The name *achernar* refers to one of the stars of the southern hemisphere (constellation of Eridanus).

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with few short unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; with median row of spinules behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others. Anterior branch of cervical groove with short setae. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, exceeding or reaching sinus between rostral and supraocular spines. Rostral spine spiniform, with thin dorsal longitudinal carina; supraocular spines well developed and more slender than rostrum (Figs. 1A, 1B).

Sternum: Thoracic sternites 4-6 with few arcuate striae; sternite 7 smooth (Fig. 1C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 1A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and slightly shorter than distolaterall; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth (Fig. 1D).

Antenna: Anterior prolongation of segment 1 slightly overreaching antennular peduncle by about one-fourth of its length. Segment 2 about twice length of segment 3 and twice longer than wide, ventral surface with scales; distomesial spine spiniform not exceeding antennal peduncle and without tuff of setae, reaching mid-length of anterior prolongation of segment 1, and clearly not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3; segment 3 nearly 1.5 times longer than wide and unarmed. (Fig. 1D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 1E).

Pereopod 1 (cheliped): Long and slender, squamate, between 4.8-4.9 times carapace length; carpus about as long as palm, and 5.9-6.5 times longer than height; palm 1.2-1.3 times fingers length. Base of carpus without bundle of setae (Fig. 1F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.1-3.2 times carapace length, merus 1.5-2.0 times longer than carapace, about 12 times as long as high, 4.5 times as long as carpus and 1.5-1.7 times as long as propodus; propodus about 11-14 times as long as high, and 1.7 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, small distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus slightly shorter than P2 merus; propodus and dactylus as long as those of P2. P4 as long as P2; merus about 1.5-2.2 times carapace length; propodus and dactylus as long as those of P3; merocarpal articulation slightly exceeding end of anterior prolongation of segment 1 of antennal peduncle (Figs. 1G, 1H, 1I).

REMARKS. — The new species is morphologically very close to *P. antares* n. sp. from New Caledonia and *P. cretata* Macpherson, 1996 from Wallis Islands and Waterwitch Bank (see the Remarks under these species).

DISTRIBUTION. — Tonga, between, 461 and 497 m.

Paramunida amphitrita Macpherson, 1996

Figs. 12B, 16A

Paramunida amphitrita Macpherson, 1996: 409, fig. 7 (Futuna Island, 233–235 m). — Macpherson, 2004: 282 (in part) (Fiji and Tonga, 327–410 m). — Baba, 2005: 301 (key, synonymies). — Baba *et al.*, 2008: 171 (list of occurrences).

Not *Paramunida amphitrita* Macpherson, 2004: 282 (Fiji, in part, specimens from Stn CP1412 = *P. cretata* Macpherson, 1996).

MATERIAL EXAMINED. — Futuna Island. MUSORSTOM 7. Stn 517, 14°13.4'S, 178°10,4'W, 12 May 1992, 233-235 m: 1 F 7.7 mm (holotype), 1 F 8.9 mm, (MNHN-Ga 3650, 3741).

Fiji Islands. BORDAU 1. Stn 1394, 16°45.19’S, 179°59.19’E, 23 February 1999, 416 m: 2 ov. F 11.4-13.0 mm. — Stn 1410, 16°05.51’S, 179°27.76’W, 26 February 1999, 400-410 m: 1 M 12.2 mm, 1 ov. F 10.5 mm. — Stn 1412, 16°05.52’S, 179°28.05’W, 26 February 1999, 400-407 m: 2 ov. F 10.5-11.2 mm.

Tonga Islands. BORDAU 2. Stn 1583, 18°36.72’S, 174°02.84’W, 13 June 2000, 327-360 m: 1 juv. 4.8 mm.

New Caledonia. Lifou island. LIFOU. Stn DW1650, 20º54.15’S, 167º01.7’E, 15 November 2000, 120-250 m: 1 M 9.2 mm, 2 ov. F 10.4-10.5 mm.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight or slightly concave. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron smooth, few striae on sternite 4. Lateral margin of antennular segment 1 with straight (distal) portion slightly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 nearly twice longer than broad, with

distomesial spine spiniform, clearly overreaching end of segment 3 but not reaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 more than twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 18 times as long as wide, and about 1.4 times dactylus length.

REMARKS. — *Paramunida amphitrita* is related to *P. cretata* Macpherson, 1996 from Waterwitch Bank, Wallis Islands and Fiji and *P. thalie* Macpherson, 1996, from Vanuatu, New Caledonia, Loyalty Islands, Chesterfield Islands, Fiji and Queensland (see below under the Remarks of these species).

DISTRIBUTION. — Futuna, Fiji, Tonga and New Caledonia, between 233 and 410 m.

Paramunida antares n.sp.
Figs. 2, 12C

TYPE MATERIAL. — *Holotype*: New Caledonia. NORFOLK 1. Stn DW1694, 24°40'S, 168°39'E, 24 June 2000, 575-582 m: 1 M 9.0 mm (MNHN-Gaxxxx).

Paratypes: New Caledonia. NORFOLK 1. Stn CP1670, 23°39'S, 167°59'E, 21 June 2000, 382-384 m: 1 M 5.0 mm, 1 F 9.2 mm (MNHN-Gaxxxx).

ETYMOLOGY. — The name *antares* refers to one of the stars of the southern hemisphere (constellation of Scorpus).

DESCRIPTION. — *Carapace*: Slightly longer than broad. Dorsal surface covered with numerous spinules and unirramous setae; setae and spinules usually not on arcuate striae. Epigastric region with 2 spines, each behind supraocular spine, and with median row of spines behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, slightly exceeding sinus between rostral and supraocular spines. Rostral spine triangular, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum (Figs. 2A, 2B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-7 smooth (Figs. 2C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with few spinules and small spines (Fig. 2A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and shorter than distolateral; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment slightly longer than second (Fig. 2D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about 1.4 times length of segment 3 and 1.5 times longer than wide, ventral surface with scales; distomesial spine spiniform with no tuff of setae

at base, reaching end of third segment, not reaching mid-length of anterior prolongation of segment 1, and not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3; segment 3 nearly twice longer than wide and unarmed (Fig. 2D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 2E).

Pereopod 1 (cheliped): No chelipeds on type material.

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.3 times carapace length, merus 1.5 times longer than carapace, about 12 times as long as high, 4.4 times as long as carpus and 1.7 times as long as propodus; propodus about 9 times as long as high, and 1.6 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, small distal spine on dorsal and ventral margin. Propodus with some small movable ventral spinules. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 as long as or slightly shorter than P2; merus about 1.4 times carapace length; propodus and dactylus slightly shorter than those of P3; merocarpal articulation clearly exceeding end of anterior prolongation of first segment of antennal peduncle (Figs. 2F, 2G, 2I).

REMARKS. — *Paramunida antares* n. sp. from New Caledonia is very close to *P. achernar* n. sp. from Tonga. The two species can be distinguished by the following characters:

— The P2-4 propodi are more than 10 times longer than high in *P. antares*, whereas the propodi are less than 10 times in *P. achernar*.

— The merocarpal articulation of P3 clearly exceeds the anterior prolongation of the antennal segment 1 in *P. antares,* whereas this articulation slightly exceeds the anterior prolongation in *P. achernar*.

The genetic divergences between *P. achernar* and *P. antares* were 3.67% (16S rRNA) and 9.69% (ND1).

The new species is also related to *P. luminata* Macpherson, 1996, from Tuscarora Bank, Wallis Islands, Alofi Bank, Bayonnaise Bank and *P. echinata* Macpherson, 2000, from the French Polynesia (see under the Remarks of these species).

The specimens identified as *P. luminata* by Machordom and Macpherson (2004) belongs to the present new species.

DISTRIBUTION. — New Caledonia, between 382 and 582 m.

Paramunida antipodes Ahyong & Poore, 2004

Fig. 16B

Paramunida antipodes Ahyong & Poore, 2004: 65, fig. 16 (Queensland and New South Wales, 420–549 m). — Poore, 2004: 238, fig. 66a (compilation). — Baba, 2005: 301 (key, synonymies). — Baba *et al.*, 2008: 171 (list of occurrences).

DIAGNOSIS (from Ahyong & Poore, 2004). — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines

slightly concave. Mesogastric region with 1 distinct spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron smooth, with few median striae on sternite 4, and some short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine mucronated, clearly overreaching end of segment 3 and nearly reaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 1.5 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9 times as long as wide, and about 1.4 times dactylus length.

REMARKS. — The species resembles *P. parvispina* n. sp. from Chesterfield Islands and *P. evexa* Macpherson, 1993 from Indonesia (see below under the Remarks of these species).

DISTRIBUTION. — Queensland and New South Wales, between 420 and 549 m.

Paramunida ascella n. sp.

Figs. 3, 12D

TYPE MATERIAL. — *Holotype*: Vanuatu. SANTO. Stn AT 9, 15°41.5'S, 167°01.3'E, 17 September 2006, 481 m: M 10.9 mm (MNHN-Gaxxxx).

Paratypes: Vanuatu. MUSORSTOM 8. Stn CP 1119: 15°08'S, 166°53'E, 09 October 1994, 254-300 m: 1 ov. F 10.7 mm (MNHN-Gaxxxx). — Stn CP 1134, 15°39'S, 167°02'E, 11 October 1994, 230-287 m: 1 M 10.0 mm, 1 ov. F 8.5 mm, 1 F 8.1 mm (MNHN-Gaxxxx). Vanuatu. SANTO. Stn AT 9, 15°41.5'S, 167°01.3'E, 17 September 2006, 481 m: 3 M 7.8-10.9 mm, 12 ov. F 9.8-11.9 mm (MNHN-Gaxxxx). — Stn AT 11, 15°39.5'S, 167°01.5'E, 17 September 2006, 272-286 m: 1 ov. F 11.5 mm (MNHN-Gaxxxx). — Stn AT 63, 15°39.6'S, 167°01.3'E, 04 October 2006, 290-334 m: 5 M 10.6-12.2 mm, 6 ov. F 9.9-12.3 mm, 1 F 8.7 mm (MNHN-Gaxxxx).

ETYMOLOGY. The name *ascella* refers to one of the stars of the southern hemisphere (constellation of Sagittarius)

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with spinules moderately numerous in gastric and hepatic regions; each spinule usually on short arcuate striae, with some unirramous setae. Epigastric region with 2 spines, each behind supraocular spine, without median row of spines behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others (third spine very reduced in some specimens). Cervical groove distinct, with long setae along anterior branch. Cardiac and anterior branchial regions circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, exceeding sinus between rostral and supraocular spines. Rostral spine triangular, supraocular spines well developed and half as long and more slender than rostrum (Figs. 3A, 3B).

Sternum: Thoracic sternite 4 with some arcuate striae; sternites 5-6 with some striae on each lateral side, sternite 7 smooth (Fig. 3C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior

ridge; posterior ridge with distinct single median spine (broken in holotype). Ridges with numerous spinules and a few small spines (Fig. 3A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and slightly shorter than distolateral; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment slightly longer than second (Fig. 3D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by one half of its length. Segment 2 about 2.5 times length of segment 3 and less than twice longer than wide, ventral surface with scales; mesial margin, including distal spine, straight; distomesial spine mucronated with few setae at base, reaching end of antennal peduncle, not reaching mid-length of anterior prolongation of segment 1 and not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3; third segment 1.5 times longer than wide and unarmed(Fig. 3D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 3E).

Pereopod 1 (cheliped): Long and slender, squamate, between 4.6-5.2 times carapace length; carpus 0.8-1.1 times palm length, and 5.5-6.2 times longer than height; palm 1.2-2.0 times fingers length. Base of carpus without bundle of setae (Fig. 3F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 2.9-3.1 times carapace length, merus 1.3-1.4 times longer than carapace, about 8.3-10.0 times as long as high, 2.4-3.8 times as long as carpus and 1.6-2.4 times as long as propodus; propodus about 8.2-10.0 times as long as high, and 1.6-2.0 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; few small spines along ventrolateral margin. Carpus with some small dorsal spines, well developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carina along mesial and lateral sides, ventral border unarmed. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 shorter than P2; merus about 1.1-1.3 times carapace length; propodus and dactylus slightly shorter than those of P3; merocarpal articulation not reaching end of anterior prolongation of segment 1 of antennal peduncle. P3-P4 dactylus with longitudinal carinae along lateral and mesial margin (Fig. 3G, 3H, 3I).

REMARKS. — *Paramunida ascella* is related to *P. crinita* n. sp. from the Philippines, and *P. mozambica* n. sp. from Mozambique (see under the Remarks of these species).

DISTRIBUTION. — Vanuatu, between 230 and 481 m.

Paramunida belone **Macpherson, 1993**

Figs. 12E, 16C

Paramunida belone Macpherson, 1993: 448, figs 1, 12 (Loyalty Islands, 250–437 m). — Macpherson, 1996: 410 (Futuna Island, 245–395 m). — Macpherson, 2004: 282 (Fiji and Tonga, 321–487 m). — Baba, 2005: 197, 302 (key, synonymies, Bali Sea, 450 m). —

Baba *et al.*, 2008: 171 (list of occurrences).

MATERIAL EXAMINED. — New Caledonia. NORFOLK 2. Stn CP2118, 23°22.87’S, 168°00.86’E, 01 November 2003, 242 m: 1 M 14.2 mm, 2 ov. F 10.5-11.5 mm.
Tonga. BORDAU 2. Stn CP1511, 21º07.83’S, 175º22.38’W, 31 May 2000, 384-402 m: 1 M 10.7 mm, 2 ov. F 10.7-11.1 mm.
Loyalty Islands. MUSORSTOM 6. Stn DW398, 20°47.19’S, 167°05.65’E, 13 February 1989, 370 m: 1 F broken.
Vanuatu. MUSORSTOM 8. Stn CP963, 20°20.10'S, 169°49.08'E, 21 September 1994, 400-440 m: 18 M 8.2-14.8 mm, 6 ov. F 10.8-13.4 mm, 1 F 5.9 mm. — Stn CP980, 19°21.02'S, 169°25.22'E, 22 September 1994, 430-450 m: 4 M 12.3-13.4 mm, 2 F 10.3-14.6 mm. — Stn CP1091, 15°10.24'S, 167°13.01'E, 06 October 1994, 344-350 m: 2 M 7.9-11.7 mm, 1 ov. F 10.2 mm.
SANTO. Stn AT1, 15°32.4’S, 167°16.4’E, 14 September 2006, 167-367 m: 2 M 12.5-12.7 mm. — Stn AT48, 15°33.8'S, 167°18.9'E, 30 September 2006, 330-341 m: 2 ov. F 10.6-11.7 mm. — Stn AT49, 15°33.8'S, 167°18.9'E, 30 September 2006, 266-328 m: 1 ov. F 8.6 mm.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight or slightly concave. Mesogastric region with 1 (rarely 2) well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron smooth, with some median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 more than 2.5 times longer than broad, with distomesial spine of segment 2 mucronated, clearly overreaching antennal peduncle, distolateral spine reaching end of segment 3; segment 3 1.5 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 13 times as long as wide, and about 1.4 times dactylus length.

REMARKS. — *Paramunida belone* is morphologically related to *P. lophia* Cabezas *et al.*, 2009, *P. salai* Cabezas *et al.*, 2009 from the Solomon Islands, and *P. spica* n. sp. from Vanuatu (see under the Remarks of these species).

The species is also related to *P. proxima* (Henderson, 1885) from the Philippines, off Zamboanga, Mindanao, N of the Admiralty Islands, Indonesia, Kei Islands, Solomon Islands and Vanuatu (see below under the Remarks of *P. proxima*).

DISTRIBUTION. — New Caledonia, Loyalty Islands, Vanuatu, Tonga, Fiji, Walis and Futuna and Bali Sea between 250 and 487 m.

***Paramunida cretata* Macpherson, 1996**

Figs. 12F, 16D

Paramunida cretata Macpherson, 1996: 411, figs 8, 23 (SW Pacific, Waterwitch Bank and Wallis Islands, 300–365 m). — Macpherson, 2004: 283 (Tonga, 371 and 497 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 171 (list of occurrences).
Paramunida amphitrita Macpherson, 2004: 282 (in part, specimens from Stn CP1412, not *P. amphitrita* Macpherson, 1996).

MATERIAL EXAMINED. — Waterwitch Bank. MUSORSTOM 7. Stn 569, 12°30.0'S, 176°51.2'W, 21 May 1992, 300-305 m: 1 ov. F 11.5 mm (holotype), 4 F 7.4-10.5 mm (MNHN-Ga 3651, 3744).

Wallis Islands. MUSORSTOM 7. Stn 583, 13°11.1'S, 176°14.2'W, 22 May 1992, 330-365 m: 2 M 10.0-11.4 mm, 1 ov. F 10.0 mm (USNM). — Stn 605, 13°21.3'S, 176°08.4'W, 26 May 1992, 335-340 m: 1 F 6.0 mm (MNHN-Ga 3745).

Fiji. BORDAU 1. Stn CP1412, 16°05.52'S, 179°28.05'W, 26 February 1999, 400-407 m: 1 ov. F 10.7 mm.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3 well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron smooth, with some median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 slightly longer than broad, with distomesial spine spiniform, overreaching end of segment 3 but not reaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 10 times as long as wide, and about 1.5 times dactylus length.

REMARKS. — This species resembles *P. achernar* n. sp. from Tonga. They can be distinguished on the basis of the following characters:

— The strong anterior prolongation on the antennal segment clearly overreaches the antennular peduncle in *P. cretata* , whereas this prolongation slightly overreaches the antennular peduncle in *P. achernar*.

— The antennal segment 2 is twice longer than wide in *P. achernar*, whereas this segment is slightly longer than wide in *P. cretata*.

— The P2 propodus is 10 times as long as high in *P. cretata*, whereas it is 11-14 times as long as high in *P. achernar*.

The genetic divergences between *P. achernar* and *P. cretata* were 2.83% (16S rRNA) and 7.57% (ND1).

Paramunida cretata is also related to *P. amphitrita* Macpherson, 1996, from Futuna, Fiji, Tonga and New Caledonia islands. The two species can be easily differentiated by the shape of the segment 3 of the antennal peduncle and the length of the distomesial spine of the segment 2. The segment 3 is as long as broad in *P. cretata,* whereas it is more than twice longer than broad in *P. amphitrita.* Furthermore the distomesial spine of the segment 2 is nearly as long as the rest of the segment in *P. amphitrita*, whereas this spine is clearly much shorter than the rest of the segment in *P. cretata.* The genetic divergences between *P. amphitrita* and *P. cretata* were 5.12% (16S rRNA) and 13.68% (ND1).

DISTRIBUTION. — Waterwitch Bank, Wallis Islands and Fiji, 300-497 m.

Paramunida crinita n.sp.

Figs. 4, 12G

Paramunida scabra Macpherson, 1993: 462 (in part, only specimens from the Philippines, MUSORSTOM 1, 2 and 3)

TYPE MATERIAL. — *Holotype*: Philippines. MUSORSTOM 2, Stn CP80, 13°45'N, 120°38'E, 01 December 1980, 178-205 m: M 7.8 mm (MNHN-Gaxxxx).

Paratypes: Philippines. MUSORSTOM 2, Stn CP80, 13°45'N, 120°38'E, 01 December 1980, 178-205 m: 15 M 6.7-8.6 mm, 11 ov. F 6.7-10.2 mm (MNHN-Gaxxxx).

MUSORSTOM 3. Stn CP90, 14°00'N, 120°19'E, 31 May 1985, 195 m: 11 M 8.6-11.2 mm, 4 F 9.2-10.6 mm (MNHN-Gaxxxx).

ETYMOLOGY. — From the Latin *crinis*, hair, in reference to the long setae along the cervical groove.

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with some unirramous setae; long and dense setae along anterior branch of cervical groove Epigastric region with 2 spines, each behind supraocular spine, with median row of minute spinules behind rostral spine. Mesogastric region with one median spine. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, clearly exceeding sinus between rostral and supraocular spines. Rostral spine spiniform, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum (Figs. 4A, 4B).

Sternum: Thoracic sternites 4-6 with some arcuate striae, sternite 7 smooth (Fig. 4C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 4A).

Eyes: Maximum corneal diameter about one-third distance between bases of anterolateral spines.

Antennule: Segment 1 exceeding corneae, with distomesial spine small and slightly shorter than distolateral; about twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and squamate, first segment slightly longer than second (Fig. 4D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about twice length of segment 3 and twice longer than wide, ventral surface with scales; distomesial spine spiniform with no tuff of setae at base, not exceeding antennal peduncle, overreaching mid-length of anterior prolongation of segment 1 and not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3; segment 3 about as long as wide and unarmed. Distomesial spine segment 2 shorter than the rest of the segment (Fig. 4D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin with distal spine (Fig. 4E).

Pereopod 1 (cheliped): Long and slender, squamate, between 5.0-5.7 times carapace length; carpus 0.8 times palm length, and 7.2-7.7 times longer than height; palm 1.5 times fingers length. Base of carpus without bundle of setae (Fig. 4F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.1-3.7 times carapace length, merus 1.4-1.5 times longer than carapace, about 10-11 times as long as high, 3.6-4.1 times as long as carpus and 1.5-1.7 times as long as propodus; propodus about 10.3-11 times as long as high, and 1.4-1.8 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well-developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus nearly reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 slightly shorter than P2; merus about 1.2-1.4 times carapace length; propodus and dactylus slightly shorter than those of P3; merocarpal articulation slightly exceeding end of anterior prolongation of segment 1 of antennal peduncle (Fig. 4G, 4H, 4I).

REMARKS. — *Paramunida crinita* n. sp. resembles *P. ascella* n. sp. from Vanuatu. The two species can be differentiated by the presence of one distinct mesogastric spine in *P. crinita*, whereas there are 3 distinct mesogastric spines in *P. ascella*. Furthermore, the distomesial spine of the antennal segment 2 is mucronated in *P. ascella*, whereas this spine is spiniform in *P. crinita*.

The genetic divergences between *P. ascella* and *P. crinita* were 1.18% (16S rRNA) and 2.51% (ND1).

DISTRIBUTION. — Philippines, between 178 and 205 m

Paramunida cristata **Macpherson, 2004**

Figs. 12H, 16E

Paramunida cristata Macpherson, 2004: 283, fig. 13 (Fiji and Vanuatu, 390–513 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 172 (list of occurrences). — Baba *et al.*, 2009: 278, fig. 254 (Taiwan, 390-403 m).

MATERIAL EXAMINED. — Fiji Islands. BORDAU 1. Stn CP 1395, 16º45.13’S, 179º59.20’E, 23 February 1999, 423-500 m: 1 ov. F 10.6 mm. — Stn CP 1447, 16145.23’S, 179º59.13’E, 04 March 1999, 420-513 m: 1 M 12.5 mm.
Taiwan. Stn CP269, 24º30.55’N, 122º05.78’E, 02 September 2004, 397-399 m: 1 F 10.1 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thick dorsal carina; margin between rostral and supraocular spines slightly concave. Mesogastric region with 1 well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine spiniform, overreaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 slightly longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9-10 times as long as wide, and about 1.3 times dactylus length.

REMARKS. — *Paramunida cristata* is morphologically related to *P. scabra* Henderson, 1885 from the western Pacific and Indian Oceans (but see the Remarks under *P. scabra*).

DISTRIBUTION. — Fiji, Vanuatu, and Taiwan between 390 and 513 m.

Paramunida curvata **Macpherson, 2004**

Figs. 12I, 16F

Paramunida curvata Macpherson, 2004: 285, fig. 14 (Fiji, 229–417 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. —Vanuatu. BOA 0. Stn CP2326, 15º39.83'S, 167º01.9'E, 18 November 2004, 260-313 m: 7 M 8.7-9.8 mm, 8 ov. F 8.1-9.9 mm, 2 F 5.3-9.1 mm.
SANTO. Stn AT34, 15°35.9'S, 167°17.1'E, 23 September 2006, 234-270 m: 1 ov. F 9.6 mm. — Stn AT47, 15°35.0'S, 167°18.3'E, 30 September 2006, 250-309 m: 4 M 8.3-10.0 mm, 1 ov. F 8.6 mm. — Stn AT121, 15°38.7'S, 167°01.2'E, 19 October 2006, 275-290 m: 3 M 8.0-9.8 mm, 4 ov. F 7.9-8.8 mm, 2 F 5.3-9.1 mm.
Fiji. MUSORSTOM 10. Stn 1390, 18º18.59'S, 178º05.10'E, 19 August 1998, 234-361 m: 1 ov. F 10.0 mm.

DIAGNOSIS. — Rostral spine smaller or at most equal than supraocular spines, with small thin dorsal carina; margin between rostral and supraocular spines convex. Mesogastric region without distinct spines. Median cardiac region with small spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with few short striae on sternite 4, smooth on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine spiniform and curved, overreaching end of antennal peduncle, distolateral spine not reaching midlength of segment 3; segment 3 elongate, 4 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 15 times as long as wide, and about 1.5 times dactylus length.

REMARKS. — *Paramunida curvata* belongs to the group of species with the rostral spine smaller than the supraocular spines. However, *P. curvata* can be differentiated from the other species of the group (*P. hawaiiensis, P. microrhina, P. setigera*, and *P. tenera*) by having the margin between rostral and supraocular spines clearly convex, whereas this margin is straight or slightly convex in the other species.

Genetically the closest relative is *P. scabra* (Henderson, 1885) from Hong Kong, East and South China Sea (Dongsha), Indonesia, Philippines, Taiwan, Japan, and Australia (off Central Queensland). The differences were 6.66 % (16S rRNA) and 9.22 % (ND1).

DISTRIBUTION. — Fiji and Vanuatu, between 229 and 417 m.

Paramunida echinata **Macpherson, 1999**

Figs. 13A, 16G

Paramunida echinata Macpherson, 1999: 420, fig. 2 (Marquesas Islands, 102–430 m). —

Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. — French Polynesia. Marquesas Islands. MUSORSTOM 9. Stn CP1176, 08º45.8'S, 140º14.5'W, 25 August 1997, 260 m: 17 M 10.8-13.4 mm, 13 ov. F 10.8-12.7 mm, 1 F 9.1 mm (MNHN-Ga 4367).

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron smooth, with some short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 more than twice longer than broad, with distomesial spine mucronated, overreaching end of segment 3, distolateral spine not reaching end of segment 3; segment 3 1.5 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 10 times as long as wide, and slightly longer than dactylus.

REMARKS. — *Paramunida echinata* is related to *P. labis* Macpherson, 1996 from Futuna and Wallis Islands, Fiji, Tonga, Chesterfield Islands, and New Caledonia (see below under the Remarks of that species) and *P. antares* n. sp. from New Caledonia.

Paramunida echinata and *P. antares* can be easily distinguished by the shape of the distomesial spine of the antennal segment 2, being slightly mucronated in *P. echinata* and spiniform in *P. antares*. The genetic divergences between *P. echinata* and *P. antares* were 2.80% (16S rRNA) and 10.92% (ND1).

DISTRIBUTION. — French Polynesia, Marquesas Islands, between 102 and 430 m.

***Paramunida evexa* Macpherson, 1993**

Figs. 13B, 16H

Paramunida evexa Macpherson, 1993: 450, fig. 2 (Indonesia, 174–226 m). — Baba, 2005: 198, 302 (key, synonymies, Ambon Sea, 128–238 m). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. — Indonesia. Kei Islands. KARUBAR. Stn CP 67, 08º58.59'S, 132º07.20'E, 01 November 1991, 233-246 m: 2 M 10.2-11.3 mm, 1 ov. F 9.0 mm. — Stn CP 82, 09º32'S, 131º02'E, 4 November 1991, 215-219 m: 1 ov. F 11.9 mm. — Stn CP 86, 09º26'S, 131º13'E, 04 November 1991, 223-225 m: 6 M 9.4-10.6 mm, 2 ov. F 10.4-11.8 mm, 4 F 8.4-11.0 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3-4 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron squamate, with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine of segment 2 blunty produced, overreaching end of segment 3, small distolateral spine not reaching

midlength of segment 3; segment 3 as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 8 times as long as wide, and about 1.3-1.4 times longer than dactylus.

REMARKS. — *Paramunida evexa* is related to *P. antipodes* Ahyong & Poore, 2004 from Eastern Australia. The two species can be easily differentiated by the following characters: the mesogastric region has only one distinct spine (rarely 2) in *P. antipodes*, whereas there is a row of 3-4 distinct mesogastric spines en *P. evexa*; the distomesial spine of the antennal segment 2 is blunty produced in *P. evexa*, whereas it ends in a distinct spine in *P. antipodes;* the sternal plastron has numerous striae in *P. evexa*, being smooth in *P. antipodes*.

Paramunida evexa is also close to *P. scabra* (Henderson, 1885), from Hong Kong, East and South China Sea (Dongsha), Indonesia, Philippines, Taiwan, Japan, and Australia (off Central Queensland) (see under the Remarks of that species).

DISTRIBUTION. — Indonesia (Ambon, Kei Islands), between 128 and 246 m.

***Paramunida granulata* (Henderson, 1885)**

Figs. 13C, 16I

Munida granulata Henderson, 1885: 409 (S of the Fiji Islands, 549 m). — Henderson, 1888: 133, pl. 14, figs 3, 3a, 3b (off Matuku, Fiji, 576 m).

Paramunida granulata. — Baba, 1988: 176, fig. 72 (Moluccas off W coast of Halmahera, 545 m). — Macpherson, 1993: 452, figs 3, 13 (New Caledonia, Loyalty Islands and Indonesia; reexamination of type material; 439–650 m). — Macpherson, 1996: 412 (SW Pacific (Futuna Island, Wallis Islands, Bayonnaise Bank), 400–450 m). — Macpherson, 2004: 287 (Fiji and Tonga, 395–592 m). — Ahyong & Poore, 2004: 68 (Queensland, 548 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. — Tonga. BORDAU 2. Stn CP1640, 21º09.14’S, 175º23.96’W, 21 June 2000, 564-569 m: 2 M 9.6-10.2 mm, 2 ov. F 9.8-12.7 mm.

Vanuatu. MUSORSTOM 8. Stn CP1027, 17°53.05'S, 168°39.35'E, 28 September 1994, 550-571 m: 6 M 7.0-12.4 mm, 1 F 10.8 mm.

Loyalty Islands. MUSORSTOM 6. Stn DW468, 21º05.86’S, 167º32.98’E, 21 February 1986, 600 m: 1 M 11.5 mm (MNHN-Ga 3218).

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight or slightly concave. Mesogastric region with 1 well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron squamate, with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine long, almost reaching end of anterior prolongation of segment 1, distolateral spine nearly reaching end of segment 3; segment 3 1.5 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 7-8 times as long as wide, and about 1.2-1.3 times longer than dactylus.

REMARKS. — *Paramunida granulata* is morphologically and genetically very different from the other species of the genus. This species is unique in having the distomesial spine of antennal

segment 2 very long, almost reaching the end of the anterior prolongation of segment 1. This distomesial spine is always much shorter in the other species of *Paramunida*.

The genetic divergences among *P. granulata* and other *Paramunida* are always greater than 8% (16S rRNA) and 16% (ND1).

DISTRIBUTION. — Philippines, Indonesia, Queensland, New Caledonia, Loyalty Islands, Fiji, Tonga, Futuna Island, Wallis Islands and Bayonnaise Bank, between 395 and 650 m.

***Paramunida hawaiiensis* (Baba, 1981)**

Figs. 13D, 17A

Munida hawaiiensis Baba, 1981: 288, figs 1, 2 (Hawaiian Islands between Laysan and Hawaii Island, 115–439 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. — Hawaii Islands, off Honolulu. Cronwell Cruise, Stn 61-1967: 2 M 8.8-9.3 mm (MNHN-Ga 1103).

DIAGNOSIS. — Rostral spine spiniform, smaller or at most equal than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight or slightly convex. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with long distomesial spine of segment 2 reaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 10 times as long as wide, and about 1.5 times longer than dactylus.

REMARKS. — *Paramunida hawaiiensis* belongs to the group of species with the rostral spine smaller than the supraocular spines. *P. hawaiiensis* is closely related to *P. microrhina* n. sp. from the Chesterfield Islands, but they can be differentiated each other by different characters (see below under the Remarks of *P. microrhina*).

DISTRIBUTION. — Hawaiian Islands, between 115 and 439 m.

***Paramunida labis* Macpherson, 1996**

Figs. 13E, 17B

Paramunida labis Macpherson 1996: 413, figs 9, 24 (SW Pacific (Futuna Island and Wallis Islands), 245–440 m). — Macpherson, 2004: 287 (Fiji and Tonga, 229–443 m). — Baba, 2005: 302 (key, synonymies). — Ahyong, 2007: 41, fig. 20A (Norfolk Ridge, 322–337 m). — Baba *et al.*, 2008: 172 (list of occurrences).

MATERIAL EXAMINED. — Chesterfield Islands. EBISCO. Stn DW2521, 22º45.38’S, 159º19.041’E, 08 October 2005, 310-313 m: 1 M 6.1 mm. — Stn DW2619, 20º06.084’S, 160º23.544’E, 20 October 2005, 490-550 m: 1 ov. F 8.5 mm.

Vanuatu. MUSORSTOM 8. Stn CP971, 20°18.87'S, 169°53.12'E, 21 September 1994, 250-351 m: 1 F 8.3 mm. — Stn CP1025, 17°49.01'S, 168°39.37'E, 28 September 1994, 385-410 m: 5 M 7.6-9.0 mm, 4 ov. F 8.4-8.8 mm, 5 F 7.7-9.6 mm. SANTO. Stn AT1, 15°32.4'S, 167°16.4'E, 14 September 2006, 167-367 m: 1 M 9.6 mm, 3 ov. F 8.7-10.4 mm, 1 F 9.6 mm. — Stn AT18, 15°41.3'S, 167°02.6'E, 21 September 2006, 321-336 m: 1 ov. F 11.0 mm. — Stn AT34, 15°35.9'S, 167°17.1'E, 23 September 2006, 234-270 m: 2 M 8.9-9.2 mm, 1 ov. F 8.0 mm, 3 F 6.5-10.2 mm. — Stn AT 48, 15°33.8'S, 167°18.9'E, 30 September 2006, 330-341 m: 2 ov. F 7.0-10.1 mm. — Stn AT 50, 15°36.8'S, 167°14.1'E, 30 September 2006, 140-153 m: 1 ov. F 10.1 mm.

Fiji. MUSORSTOM 10. Stn CP1390, 18º18.59'S, 178º05.10'E, 19 August 1998, 234-361 m: 2 M 9.0-10.4 mm, 1 ov. F 9.8 mm.

Tonga. BORDAU 2. Stn CP1572, 19º42.31'S, 174º31.35'W, 11 June 2000, 391-402 m: 2 ov. F 8.0-8.5 mm.

Wallis Islands. MUSORSTOM 7. Stn 612, 13°21.4'S, 176°08.9'W, 26 May 1992, 255 m: 1 M 7.0 mm, 4 F 4.1-5.6 mm (MNHN-Ga 3753).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad, with distomesial spine mucronated having bundle of terminal setae, slightly overreaching end of segment 3, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 10 times as long as wide, and slightly longer than dactylus.

REMARKS. — The species is closely related to *P. echinata* Macpherson, 1999, from French Polynesia. The two species can be easily differentiated by the following characters: the rostral spine is triangular in *P. echinata*, whereas it is spiniform in *P. labis*; the P2-4 propodi are more than 1.5 times dactylus length in *P. echinata*, whereas they are slightly longer than dactyli in *P. labis*.

Paramunida labis also resembles *P. antares* n. sp. from New Caledonia. Both species can be distinguished by the shape of the distomesial spine of the antennal segment 2, being slightly mucronated in *P. echinata* and spiniform in *P. antares*.

The genetic divergences between *P. echinata* and *P. antares* were 2.80% (16S rRNA) and 10.92% (ND1). The divergences between *P. echinata* and *P. labis* were 3.17% (16S rRNA) and 8.49% (ND1).

DISTRIBUTION. — Futuna Island and Wallis Islands, Fiji and Tonga, Chesterfield Islands, New Caledonia and Norfolk Ridge between 229 and 443 m.

Paramunida leptotes **Macpherson & Baba, 2009**

Figs. 13F, 17C

Munida proxima Baba, 1982: 110, fig. 4 (Izu Shoto, 430 m). — Baba in Baba *et al.*, 1986: 173, 291, fig. 124 (Kyushu-Palau Ridge and off Amami-oshima of the Ryukyus, 320–400 m). — Wu *et al.*, 1998: 143, figs 40, 42F (Taiwan). — Baba, 2005: 199 (remarks) (not

Paramunida proxima (Henderson, 1885)).

Paramunida leptotes Macpherson & Baba, 2009: 63, figs. 5, 6 (Izu Shoto, 430 m, Kyushu-Palau Ridge and off Amami-oshima of the Ryukyus, 320–400 m, Taiwan, 300 m). — Baba *et al.*, 2009: 279, figs. 255-256 (Taiwan, 456 m).

MATERIAL EXAMINED. — TAIWAN. NE Taiwan, Stn CD 380, 24°38.598'N, 122°10.436'E, 25 July 2007, 456 m: 1 M10.3 mm (holotype) NTOU A00891. NE Taiwan, Su-ao, Yilan County, 22 May.1990: 1 ov. F 12.8 mm (paratype) NTOU A00892.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 1 well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron squamate, with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad with distomesial spine spiniform clearly exceeding antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9.5-10 times as long as wide, and 1.3-1.4 times dactylus length.

REMARKS. — The species resembles *P. proxima* (Henderson, 1885) from the Philippines, off Zamboanga, Mindanao, N of Admiralty Islands, Indonesia, Kei Islands, Solomon Islands and Vanuatu, and *P. polita* Macpherson, 1993 from Indonesia, Philippines, Kei Islands and Moro Gulf off Zamboanga (see below under the Remarks of these species).

DISTRIBUTION. — Izu Shoto, Kyushu-Palau Ridge and off Amami-oshima of the Ryukyus, Taiwan and Japan, between 320 and 456 m.

***Paramunida longior* Baba, 1988**

Figs. 13G, 17D, E

Paramunida longior Baba, 1988: 177, fig. 73 (Moluccas off W coast of Halmahera and South China Sea off SW Luzon, 340–485 m). — Macpherson, 1993: 454, figs 3, 13 (New Caledonia and Indonesia, 250–502 m). — Komai, 2000: 360 (list). — Macpherson, 2000: 2004: 287 (Fiji and Tonga, 384–520 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 173 (list of occurrences).

MATERIAL EXAMINED. — New Caledonia. MUSORSTOM 4. Stn 173, 19°02.50'S, 163°18.80'E, 17 September 1985, 250-290 m: 1 M 5.5 mm (MNHN-Ga 3221). — Stn 243, 22°02.80'S, 167°07.70'E, 02 October 1985, 435-450 m: 5 M 7.1-8.0 mm, 17 F 4.8-8.6 mm (MNHN-Ga 3222). — Stn. 245, 22°07.00'S, 167°11.00'E, 3 October 1985, 415-435 m: 3 M 7.9-8.2 mm, 4 ov. F 8.2-8.7 mm, 1 F 7.4 mm. BATHUS 2, Stn CP 742, 22°33.45'S, 166°25.86'E, 13 May 1993, 340-470 m: 4 M 8.1-9.6 mm, 5 ov. F 8.2-9.3 mm, 2 F 7.7-8.2 mm. HALIPRO 1. Stn. CP 864, 21°29' S, 166°19' E, 22 March 1994, 430 m: 5 M 8.9-9.7 mm (one specimen with broken carapace), 1 ov. F 11.4 mm, 2 F 7.7-9.4 mm.

Solomon Islands. SALOMON 2, Stn CP 2199, 7º43.3'S, 158º29.6'E, 25 October 2004, 296-304 m: 1 ov. F 10.6 mm. — Stn CP 2272, 8º32.12'S, 157º44.38'E, 5 November 2004, 380-537 m: 2 M 7.9-9.8 mm, 1 ov. F 8.3 mm, 1 F 8.1 mm.

Fiji. BORDAU 1, Stn CP 1505, 18°12,29'S, 178°37,34'W, 13 March 1999, 420-450 m: 1 M 10.2 mm (specimen *P. aff. longior*, possible new species).

Tonga. BORDAU 2, Stn CP 1511, 21°08'S, 175°22'W, 31 May 2000, 384-402 m: 1 M 10.3 mm, 8 ov. F 7.8-10.1 mm.

DIAGNOSIS. — Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with some unirramous setae. Rostral spine triangular, without thin dorsal longitudinal carina; supraocular spines short and less than half as long and more slender than rostrum. Mesogastric and cardiac regions without median row of spines. Thoracic sternites 4-5 with few arcuate striae; sternites 6-7 smooth. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Anterior prolongation of antennal segment 1 of peduncle slightly overreaching antennular peduncle; segment 2 about 1.5 times length of segment 3 and nearly twice longer than wide, distomesial spine spiniform, slightly overreaching antennal peduncle; segment 3 nearly three times longer than wide and unarmed. Base of P1 carpus without bundle of setae. P2 propodus about 23-24 times as long as high, and 1.9-2.0 times dactylus length.

REMARKS. — The present material agrees quite well with the original description and illustrations (Baba, 1988), as well as the additional illustrations of the holotype kindly provided by K. Baba. However, in the present material the distomesial spine of the antennal segment 2 is slightly smaller than in the types. It will be interesting to collect additional topotypic material in order to confirm the constancy of this difference. The male collected in Fiji (BORDAU 1, Stn CP 1505) is genetically very different than the other specimens (1.99% divergence in 16S rRNA and 7.39% in ND1), suggesting the existence of a different species. Unfortunately this specimen is seriously damaged, avoiding an adequate description.

Paramunida longior is closely related to those species with very long and slender walking legs, e.g. *P. curvata, P. setigera* and *P. tenera*. However, *P. longior* has the supraocular spines shorter than the rostral spine, whereas the rostral spine is always smaller or at most equal than the supraocular spines. Furthermore, the P2-4 propodi are particularly slender (ca. 20 times as long as high) in *P. longior*, whereas they are less slender (7-14 times) in the other species. The genetic divergences between *P. longior* and the other species were always larger than 6% (16S rRNA) and 12% (ND1).

DISTRIBUTION. — Moluccas off W coast of Halmahera and South China Sea off SW Luzon, Indonesia, New Caledonia, Fiji, Tonga and Solomon Islands, between 250 and 537 m.

Paramunida lophia Cabezas, Macpherson & Machordom, 2009

Figs. 13H, 17F

Paramunida lophia Cabezas *et al.*, 2009: 478, fig. 6 (Solomon Islands, 135-325 m).

MATERIAL EXAMINED. — Solomon Islands. SALOMON 1, Stn 1831, 10°12.1'S, 161°19.2'E, 05 October 2001, 135–325 m: 1 M 10.2 mm (holotype, MNHN-Ga6512), 2M 13 mm (paratypes, MNHN-Ga6513). SALOMON 2, Stn 2191, 08º23.8’S, 159º27.1’E, 24 October 2004, 300 m: 1 ov. F 10.2 mm (paratype, MNHN-Ga6514). — Stn 2199, 7º43.3’S, 158º29.6’E, 25 October 2004, 296–304 m: 3 M 9.1-11.8 mm (paratypes, MNHN-Ga6515).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3

distinct spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 nearly twice longer than broad with distomesial spine mucronated, clearly overreaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9.5-10 times as long as wide, and 1.2-1.4 times dactylus length.

REMARKS. — This species is closely related to *P. belone* Macpherson, 1993, from New Caledonia, Loyalty Islands, Vanuatu, Tonga, Fiji, Walis and Futuna.

The two species can be distinguished by the following aspects:

— There is one (rarely 2) mesogastric spine in *P. belone,* whereas there is a row of 3 or 4 spines in *P. lophia*.

— The spines of the antennal segment 2 are different in the two species. The distolateral spine overreaches the end of the segment 3 in *P. belone*, whereas this spine only reaches midlength of the segment 3 in *P. lophia*.

— The distomesial spine of the antennal segment 2 clearly exceeds the end of the antennal peduncle and reaches or slightly overreaches the basal segment of the antennular peduncle in *P. belone*; whereas this spine overreaches the end of the antennal peduncle but clearly not reach the end of the basal segment of the antennular peduncle in *P. lophia* (Cabezas *et al.*, 2009).

The genetic divergences between *P. belone* and *P. lophia* were 1.71% (16S rRNA) and 4.56% (ND1).

DISTRIBUTION. — Solomon Islands, between 135 and 325 m.

***Paramunida luminata* Macpherson, 1996**

Figs. 13I, 17G

Paramunida luminata Macpherson, 1996: 415, figs 10, 25 (SW Pacific, Tuscarora Bank, Wallis Islands, Alofi Bank, Bayonnaise Bank, 400–440 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 173 (list of occurrences).

MATERIAL EXAMINED. — Bayonnaise Bank. MUSORSTOM 7. Stn 629, 11º53.7’S, 179º32.3’W, 29 May 1992, 400-420 m: 3 M 11.8-12.6 mm, 2 F 10.1-12.3 mm (MNHN-Ga 3757).

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 twice longer than broad with distomesial spine spiniform reaching end of segment 3, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida luminata* is closely related to *P. antares* n. sp. from New Caledonia. However, they can be differentiated by the presence of a median row of small spines behind the rostral spine in *P. luminata*, whereas this row is absent in *P. antares*. The genetic divergences were 1.90% (16S rRNA) and 5.49% (ND1).

DISTRIBUTION. — Tuscarora Bank, Wallis Islands, Alofi Bank and Bayonnaise Bank, between 400 and 440 m.

Paramunida marionis n.sp.
Figs. 5, 14A

TYPE MATERIAL. — *Holotype*: SW Indian Ocean, S of Madagascar. MD08, CP47, 33º11'S, 44º00'E, 16 March 1976, 620-637 m: M 10.7 mm (MNHN-Gaxxxx).

Paratypes: SW Indian Ocean, S of Madagascar. MD08, CP47, 33º11'S, 44º00'E, 16 March 1976, 620-637 m: 6 M 8.6-11.4 mm, (MNHN-Gaxxxx).

ETYMOLOGY. — The name is referred to the Research Vessel "Marion Dufresne".

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with few short unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; usually with median row of small spines behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and setae on anterior half. Anterolateral spine well developed, clearly exceeding sinus between rostral and supraocular spines. Rostral spine spiniform, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum (Figs. 5A, 5B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-6 with a few striae on each lateral side, sternite 7 smooth (Fig. 5C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4-6 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 5A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and slightly shorter than distolateral; more than twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment as long as second (Fig. 5D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about half of its length. Segment 2 about 1.5 times length of segment 3 and twice longer than wide, ventral surface with few scales; distomesial spine spiniform with no tuff of setae at base, nearly reaching end of antennal peduncle, reaching mid-length of anterior prolongation of segment 1, and not reaching end of basal segment of antennule, distolateral spine reaching

end of segment 3; third segment 1.5 times longer than wide and unarmed (Fig. 5D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 5E).

Pereopod 1 (cheliped): Long and slender, squamate, between 4.2-4.6 times carapace length; carpus 0.9-1.0 times palm length, and 5.2 times longer than height; palm 1.2-1.3 times fingers length. Base of carpus without bundle of setae (Fig. 5F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.1-3.2 times carapace length, merus 1.3-1.5 times longer than carapace, about 9.6-11 times as long as high, 3.5-4.0 times as long as carpus and 1.5-1.6 times as long as propodus; propodus about 9-11 times as long as high, and 1.5-1.9 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 shorter than P2; merus about 1.1-1.2 times carapace length; propodus and dactylus slightly shorter than those of P3; merocarpal articulation reaching end of anterior prolongation of segment 1 of antennal peduncle.

REMARKS. — The new species is closely related to the species *P. tricarinata* (Alcock, 1894) from the Arabian Sea, Maldives Islands, Andaman Sea, Taiwan and the Philippines (see under the Remarks of that species).

DISTRIBUTION. — Only known from the type locality, south of Madagascar, between 620 and 637 m.

Paramunida microrhina n.sp.

Figs. 6, 14B

TYPE MATERIAL. — *Holotype*: Chesterfield Islands. EBISCO, CP2562, 20º30.108’S, 158º42.035’E, 13 October 2005, 196-213 m: ov. F 5.1 mm (MNHN-Gaxxxx).

Paratypes: Chesterfield Islands. EBISCO, CP2562, 20º30.108’S, 158º42.035’E, 13 October 2005, 196-213 m: 5 ov. F 4.8-5.3 mm, 1 F 6.1 mm. — Stn CP2563, 20º28.900’S, 158º41.400’E, 13 October 2005, 235-280 m: 1 ov. F 5.8 mm, 1 F 7.3 mm.

ETYMOLOGY. — From the Greek, *rhinos*, nose, and *micros*, small, referring to the small rostral spine.

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on very short arcuate striae, with few small unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; withouth median row of spines behind rostral spine. Mesogastric region with small median spine. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of moderate-sized spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral small

spine, nearly reaching sinus between rostral and supraocular spines. Rostral spine short and triangular, with thin dorsal longitudinal carina; supraocular spines short and as long as the rostrum (Figs. 6A, 6B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-6 with few striae on each lateral side (Fig. 6C).

Abdomen: Abdominal somites 2-3 each with 4 moderate-sized spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4-6 spines on anterior ridge; posterior ridge without distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 6A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 exceeding corneae, with distomesial spine as long as the distolateral; about twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment longer than second (Fig. 6D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about twice length of segment 3 and 1.5 times longer than wide, ventral surface with small scales; distomesial spine very small with no tuff of setae at base, cleary not reaching midlength of segment 3, and clearly not reaching mid-length of anterior prolongation of segment 1, and end of basal segment of antennule, distolateral spine small not reaching midlength of segment 3; segment 3 as long as wide and unarmed(Fig. 6D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing one spine; merus with median and small spine on flexor margin; extensor margin unarmed (Fig. 6E).

Pereopod 1 (cheliped): Long and slender, squamate, between 6.6-7.0 times carapace length; carpus 0.8-0.9 times palm length, and 14.5-15.1 times longer than height; palm nearly twice fingers length. Base of carpus without bundle of setae (Fig. 6F).

Pereopods 2-4: Long and slender, with scales on ventro lateral sides of meri and carpi and few scales on propodi; scales with short setae. P2 4.0-4.1 times carapace length, merus 1.7-1.8 times longer than carapace, about 16-19 times as long as high, 4.2-4.4 times as long as carpus and 1.5-1.7 times as long as propodus; propodus about 12-14 times as long as high, and 1.6-1.7 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, small distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus slightly longer than P2 merus; propodus and dactylus longer than those of P2. P4 as long as P2 length; merus about 1.9-2.0 times carapace length; propodus and dactylus slightly longer than those of P3; merocarpal articulation clearly exceeding end of anterior prolongation of first segment of antennal peduncle (Figs. 6G, 6H, 6I).

REMARKS. — The new species is close to *P. hawaiiensis* (Baba, 1981) from the Hawaii Islands, both species can be easily differentiated by the following characters:

- — The antennal segment 2 has a minute distomesial spine in the new species, whereas this spine is well developed in *P. hawaiiensis*.
- — The distolateral spine of the antennal segment 2 clearly not exceeding the end of the antennal segment 3 in the new species, whereas this spine almost reaches the end of

the antennal segment 3 in *P. hawaiiensis*.

— The antennal segment 3 is twice longer than wide in *P. hawaiiensis,* whereas it is as long as wide in the new species.

— The mesogastric region has 3 well-developed spines in *P. hawaiiensis*, whereas this region only has a small median spine in the new species.

DISTRIBUTION. — Chesterfield Islands, between 196 and 280 m.

Paramunida mozambica n.sp.
Figs. 7, 14C

TYPE MATERIAL. — *Holotype:* Mozambique, MAINBAZA. Stn CC3162, 35º42’07’’S, 24º04’10’’E, 15 April 2009, 344 m: ov. F 6.9 mm (MNHN-Gaxxxx).

Paratypes: Mozambique, MAINBAZA. Stn CC3162, 35º42’07’’S, 24º04’10’’E, 15 April 2009, 344 m: 1 M 7.6 mm, 2 ov. F 6.9-7.8 mm, 1 F 6.3 mm (MNHN-Gaxxxx).

ETYMOLOGY. — From Mozambique, in reference to the area of occurrence of the species.

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on very short arcuate striae, with some short and long unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; with median row of spines behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, exceeding sinus between rostral and supraocular spines. Rostral spine spiniform, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum (Figs. 7A, 7B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-6 with few lateral arcuate striae, sternite 7 smooth (Fig. 7C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 7A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and as long as distolateral; twice longer than wide and with few setae; distal part, measured between lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment slightly longer than second (Fig. 7D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about twice length of segment 3 and twice longer than wide, ventral surface with scales; distomesial spine mucronated with lateral margin with iredescent long setae and no tuff of setae at base, not reaching or nearly reaching end of antennal peduncle, reaching mid-length of anterior prolongation of segment 1, and not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3;

segment 3 nearly twice longer than wide and unarmed (Fig. 7D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing spine; merus with median well developed spine on flexor margin; extensor margin with distal spine (Fig. 7E).

Pereopod 1 (cheliped): Long and slender, squamate, between 4.5-4.8 times carapace length; carpus 1.1 times palm length, and 5.2-6.1 times longer than height; palm 1.2-1.3 times fingers length. Base of carpus without bundle of setae (Fig. 7F).

Pereopods 2-4: Long and slender, with scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.2-3.3 times carapace length, merus 1.4 times longer than carapace, about 11-13 times as long as high, 3.6-4.3 times as long as carpus and 1.5-1.6 times as long as propodus; propodus about 8-11 times as long as high, and 1.3-1.7 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 slightly longer than P2; merus about 1.3-1.4 times carapace length; propodus and dactylus similar in length than those of P3; merocarpal articulation slightly exceeding end of anterior prolongation of segment 1 of antennal peduncle.

REMARKS. — The new species is closely related *P. ascella* n. sp. from Vanuatu. The two species can be differentiated by the following characters:

— The rostral spine is triangular in *P. ascella*, being spiniform in *P. mozambica*.

— The gastric region has more spinules in *P. mozambica* than in *P. ascella*.

The genetic divergences between *P. ascella* and *P. mozambica* were 7.90% (16S rRNA) and 11.47% (ND1).

The species is also close to *P. scabra* (Henderson, 1885) (see below under the Remarks of that species).

DISTRIBUTION. — Mozambique, at 344 m.

Paramunida parvispina n. sp.
Figs. 8, 14D

TYPE MATERIAL. — *Holotype*: Chesterfield Islands. EBISCO, Stn CP2571, 20º26.15’S, 158º45.06’E, 14 October 2005, 298-309 m: ov. F 7.0 mm (MNHN-GaXXXX).

Paratypes: Chesterfield Islands. EBISCO, Stn CP2571, 20º26.15’S, 158º45.06’E, 14 October 2005, 298-309 m: 11 M 6.5-8.2 mm, 13 ov. F 7.0-7.4 mm, 2 F 7.3-8.3 mm.

ETYMOLOGY. — From the Latin *parvus*, little, in reference to the small median gastric spine.

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on very short arcuate striae, with few short unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; withouth median row of spines behind rostral spine. Mesogastric region with small median spine. Cervical groove slightly distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region

with a median row of 3 small spines, first thicker than others. Each branchial region with row of small spines near cardiac region. Frontal margin slightly concave. Lateral margins slightly convex, with some spines and setae on anterior half. Anterolateral spine well developed, reaching sinus between rostral and supraocular spines. Rostral spine triangular, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum (Figs. 8A, 8B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-6 smooth or with 1-2 short striae on each lateral side, sternite 7 smooth (Fig. 8C)..

Abdomen: Abdominal somites 2-3 each with 4 small spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 small spines on anterior ridge; posterior ridge with distinct single small median spine. Ridges with numerous spinules and a few small spines (Fig. 8A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 slightly exceeding corneae, with distomesial spine small and slightly shorter than distolateral; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment slightly longer than second (Fig. 8D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by one-fourth of its length. Segment 2 about twice length of segment 3 and twice longer than wide, ventral surface with few scales; distomesial spine mucronated with very small point and no tuff of setae at base, only reaching end of third segment, nearly reaching mid-length of anterior prolongation of segment 1, and clearly not reaching end of basal segment of antennule, distolateral spine clearly not reaching end of segment 3; third segment 1.5 times longer than wide and unarmed (Fig. 8D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing one spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 8E).

Pereopod 1 (cheliped): Long and slender, squamate, between 6.2-6.6 times carapace length; carpus 0.8-1.1 times palm length, and 10-11.6 times longer than height; palm 1.4-1.5 times fingers length. Base of carpus without bundle of setae (Fig. 8F).

Pereopods 2-4: Long and slender, with scales on lateral sides of meri and carpi and few scales on propodi; scales with short setae. P2 3.7-4.1 times carapace length, merus 1.7-1.8 times longer than carapace, about 13-17 times as long as high, 3.5-4.0 times as long as carpus and 1.5-1.8 times as long as propodus; propodus about 11-15 times as long as high, and 1.6-2.1 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, small distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus as long or slightly longer than those of P2. P4 slightly shorter than P2; merus about 1.4-1.5 times carapace length; propodus and dactylus similar in length than those of P3; merocarpal articulation clearly exceeding end of anterior prolongation of first segment of antennal peduncle (Figs. 8G, 8H, 8I).

REMARKS. — The species resembles *P. antipodes* Ahyong & Poore, 2004, from Queensland and New South Wales. Both species can be differentiated by several characters:

— *P. antipodes* has one well-developed mesogastric spine (rarely two), whereas this

distinct spine is very small in *P. parvispina.*

— The distomesial spine of the antennal segment 2 clearly overreaches the end of the antennal segment 3 in *P. antipodes*, whereas this spine only reaches the end of the segment 3 in *P. parvispina*.

DISTRIBUTION. — Chesterfield Islands, between 298 and 309 m.

Paramunida pictura Macpherson, 1993

Figs. 14E, 17H

Paramunida pictura Macpherson, 1993: 454, figs 4, 14 (Chesterfield Islands, New Caledonia, Loyalty Islands, and Matthew & Hunter Islands, 205–600 m). — Macpherson, 1996: 416 (SW Pacific (Wallis Islands), 255–340 m). — Macpherson, 2004: 289 (Fiji and Tonga, 310–710 m). — Baba, 2005: 302 (key, synonymies). — Baba *et al.*, 2008: 173 (list of occurrences).

Not *Paramunida pictura* Macpherson, 2006: 325 (French Polynesia. Austral Archipelago, 200–500 m (= *P. poorei* n.sp.).

MATERIAL EXAMINED. — Fiji. BORDAU 1. Stn DW1417, 16º27’S, 178º55’W, 27 February 1999, 353 m: 2 M 8.7-10.0 mm, 2 ov. F 8.5-9.4 mm, 5 F 7.6-8.9 mm.

Vanuatu. MUSORSTOM 8. Stn CP963, 20°20.10'S, 169°49.08'E, 21 September 1994, 400-440 m: 1 ov. F 8.2 mm, 1 F 8.6 mm. — Stn CP1025, 17°49.01'S, 168°39.37'E, 28 September 1994, 385-410 m: 4 M 9.1-9.8 mm, 2 ov. F 7.9-8.0 mm.

New Caledonia. NORFOLK 1. Stn CP1721, 23°19'S, 168°01'E, 26 June 2001, 416-430 m: 2 M 8.8-10.2 mm.

Loyalty Islands. MUSORSTOM 6. Stn DW479, 21º09.13’S, 167º54.95’E, 22 February 1989, 310 m: 1 M 11.2 mm, 1 ov. F 9.2 mm, 2 F 8.3-8.5 mm.

Chesterfield Islands. EBISCO. Stn CP2522, 22º45.92’S, 159º19.53’E, 09 October 2005, 310-318 m: 1 M 8.4 mm. — Stn CP2632, 21º03.655’S, 160º44.673’E, 21 October 2005, 297-378 m: 2 ov. F 7.4-7.5 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 3 well developed spines. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with few short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 more than 3 times longer than broad with distomesial spine spiniform, reaching or slightly overreaching end of segment 3, distolateral spine not reaching end of segment 3; segment 3 about 1.5 times as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 8 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida pictura* is closely related to *P. poorei* from French Polynesia (Austral Islands) (see below under the Remarks of *P. poorei*).

DISTRIBUTION. — Chesterfield Islands, New Caledonia, Loyalty Islands, and Matthew & Hunter Islands, Vanuatu, Fiji, Tonga and Wallis Islands, between 205 and 710 m.

Paramunida polita Macpherson, 1993

Figs. 14F, 17I

Paramunida polita Macpherson, 1993: 456, fig. 5 (Indonesia, 281–502 m). — Baba, 2005: 198, 302 (key, synonymies, Kei Islands and Moro Gulf off Zamboanga, 200–366 m). — Baba *et al.*, 2008: 173 (list of occurrences).

MATERIAL EXAMINED. — Indonesia. Kei Islands. KARUBAR. Stn CP06, 05°49'S, 132°21'E, 22 October 1991, 287-298 m: 8 M 8.7-14.2 mm, 7 F 10.1-15.0 mm. — Stn CP25, 05°30'S, 132°52'E, 26 October 1991, 336-346 m: 2 M 10.4-11.6 mm, 3 F 9.6-10.6 mm. — Stn CP35, 06°08'S, 132°45'E, 27 October 1991, 390-502 m: 1 M 11.6 mm, 1 ov. F 12.4 mm.
Philippines. MUSORSTOM 1. Stn 20, 13°59'N, 120°20'E, 21 March 1976, 208-222 m: 1 ov. F 7.0 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; with row of small epigastric spines behind rostral spine; margin between rostral and supraocular spines straight. Mesogastric region with 1 well developed spine. Median cardiac region with 3-4 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with few short median striae on sternite 4, and few short lateral striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 about 1.3 times longer than broad with distomesial spine spiniform, slightly overreaching end of segment 3, distolateral spine nearly reaching end of segment 3; segment 3 about 1.5 times as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 6-7 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida polita* is closely related to *P. leptotes* Macpherson & Baba, 2009, from Japan and Taiwan. Both species can be easily distinguished by the length of the distomesial spine of the antennal segment 2, which clearly exceeds the antennal peduncle in *P. leptotes*, whereas this spine at most slightly exceeds the antennal peduncle in *P. polita*. The genetic divergences between *P. leptotes* and *P. polita* were 3.84% (16S rRNA) and 12.81% (ND1).

DISTRIBUTION. — Indonesia, Kei Islands, Philippines and Moro Gulf off Zamboanga, between 200 and 502 m.

Paramunida poorei n.sp.

Figs. 9, 14G

Paramunida pictura Macpherson, 2006: 325 (not *P. pictura* Macpherson, 1993).

TYPE MATERIAL. — *Holotype*: Stn DW 1999, 22°24.81'S, 151°22.17'W, 23 November 2002, 270-500 m: M 9.3 mm (MNHN-Ga xxx).

Paratypes: French Polynesia. BENTHAUS. Stn DW 1973, 23°23.49'S, 150°43.87'W, 21 November 2002, 200-350 m: 1 M 7.4 mm. — Stn DW 1995, 22°28.96'S, 151°21,85'W, 23 November 2002, 212-450 m: 1 ov. F 8.8 mm, 1 F 4.0 mm.

ETYMOLOGY. — This species name is dedicated to Gary Poore, for his contributions to the crustacean taxonomy.

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with few short unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; with median row of small spines behind rostral spine. Mesogastric region with median row of 3 spines, first thicker than others. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well-developed spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, nearly reaching sinus between rostral and supraocular spines. Rostral spine triangular, with thin dorsal longitudinal carina; supraocular spines well developed and half as long and more slender than rostrum. Margin between rostral and supraocular spines straight (Figs. 9A, 9B).

Sternum: Thoracic sternite 4 with few and small arcuate striae; sternites 5-7 smooth (Fig. 9C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with some spinules (Fig. 9A).

Eyes: Maximum corneal diameter about one-third distance between bases of anterolateral spines.

Antennule: Segment 1 exceeding corneae, with distomesial spine small and slightly shorter than distolateral; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth, first segment slightly longer than second (Fig. 9D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about 2.6 times length of segment 3 and three times longer than wide, ventral surface without scales; distomesial spine spiniform with no tuff of setae at base, not reaching end of segment 3, reaching mid-length of anterior prolongation of segment 1 although not reaching end of basal segment of antennule, distolateral spine not reaching end of segment 3; segment 3 twice longer than wide and unarmed (Fig. 9D).

Maxilliped 3: Ischium about 1.5 times length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 9E).

Pereopod 1 (cheliped): Long and slender, squamate, between 6.8-7.9 times carapace length; carpus 0.8-0.9 times palm length, and 8.5-9 times longer than height; palm 1.5-1.6 times fingers length. Base of carpus without bundle of setae (Fig. 9F).

Pereopods 2-4: Long and slender, with some scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.6-3.7 times carapace length, merus 1.7-1.8 times longer than carapace, about 14-15 times as long as high, 4.5-4.6 times as long as carpus and 1.6-1.7 times as long as propodus; propodus about 10-12 times as long as high, and 1.6-1.8 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus clearly reaching end of P1 merus. P3 with

similar spination and segment proportions than P2; merus slightly shorter than P2 merus; propodus and dactylus slightly longer than those of P2. P4 slightly shorter than P2; merus about 1.5-1.7 times carapace length; merocarpal articulation clearly exceeding end of anterior prolongation of segment 1 of antennal peduncle (Figs. 9G, 9H, 9I).

REMARKS. — The new species is closely related to *P. pictura* Macpherson, 1993 from New Caledonia, Chesterfield, Loyalty, Matthew & Hunter, Vanuatu, Fiji, Tonga and Wallis islands (Macpherson, 1993; 1996). Both species can be distinguished by the length of the distomesial spine of the antennal segment 2, since this spine reaches or slightly overreaches the end of the antennal segment 3 in *P. pictura*, whereas this spine never reaches the end of segment 3 in *P. poorei*. The genetic divergences were 2.72% (16S rRNA) and 9.76% (ND1).

DISTRIBUTION. — French Polynesia, Austral Islands, between 200 and 500 m.

***Paramunida pronoe* Macpherson, 1993**

Figs. 14H, 18A

Paramunida pronoe Macpherson, 1993: 458, fig. 6 (New Caledonia, 500–510 m). — Macpherson, 2004: 289 (Tonga, 439–497 m). — Baba, 2005: 303 (key, synonymies). — Baba *et al.*, 2008: 173 (list of occurrences).

MATERIAL EXAMINED. — New Caledonia. BATHUS 3. Stn CP833, 23°02.75'S, 166°58.23'E, 30 November 1993, 441-444 m: 1 F 4.9 mm.
NORFOLK 1. Stn CP1670, 23°39'S, 167°59'E, 21 June 2001, 382-386 m: 3 M 7.5-7.7 mm, 6 ov. F 6.6-8.3 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 1 small median spine. Median cardiac region with 1 median well developed spine. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 about 1.1-1.3 times longer than broad with distomesial spine spiniform, slightly overreaching end of segment 3, distolateral spine nearly reaching end of segment 3; segment 3 about 1.2-1.4 times as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 8 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida pronoe* belongs to the group of species with the rostral spine longer than the supraocular spines and only one distinct spine on the mesogastric region. The species is easily differentiated from the other species of the group by the presence of only one cardiac spine, whereas the other species have always a row of 3-4 spines.

Genetically the divergences among *P. pronoe* and other species were always larger than 5% (16S rRNA) and 10% (ND1).

DISTRIBUTION. — New Caledonia and Tonga, between 439 and 510 m.

***Paramunida proxima* (Henderson, 1885)**
Figs. 14I, 18B

Munida proxima Henderson, 1885: 410 (N of the Admiralty Islands, 275 m). — Henderson, 1888: 135, pl. 13, figs 2, 2a, 2b (N of Papua, 275 m). — Tirmizi, 1975: 305, figs 1–8 (designation and description of lectotype).

Paramunida proxima. — Macpherson, 1993: 460, fig. 7 (Philippines and Indonesia; reexamination of syntypes (= 2 paralectotypes), 210–306 m). — Komai, 2000: 360 (list). — Baba, 2005: 199, 303 (key, synonymies, Moro Gulf off Zamboanga and Mindanao, 293–366 m). — Baba *et al.*, 2008: 173 (list of occurrences).

Not *Munida proxima*. — Baba, 1982: 110, fig. 4 (Izu Shoto, 430 m). — Baba in Baba *et al.*, 1986: 173, 291, fig. 124 (Kyushu-Palau Ridge and off Amami-oshima of the Ryukyus, 320–400 m). — Wu *et al.*, 1998: 143, figs 40, 42F (Taiwan) (= *P. leptotes* Macpherson & Baba, 2009).

MATERIAL EXAMINED. — Philippines. MUSORSTOM 1. Stn 40, 13°57'N, 120°18'E, 23 March 1976, 265-287 m: 1 ov. F 10.5 mm.

MUSORSTOM 3. Stn 119, 12°00'N, 121°13'E, 3 June 1985, 320-337 m: 1 ov. F 11.7 mm.

Indonesia. Kei Islands. KARUBAR. Stn CP25, 05°30'S, 132°52'E, 26 October 1991, 336-346 m: 1 M 10.6 mm, 1 ov. F 11.1 mm, 1 F 9.4 mm.

Vanuatu. MUSORSTOM 8. Stn CP1107, 15°05.64'S, 167°15,31'E, 07 October 1994, 397-402 m: 2 ov. F 9.0-9.4 mm.

Solomon Islands. SALOMON 1. Stn CP1831, 10°12.1'S, 161°19.2'E, 05 October 2001, 135-325 m: 1 M 11.6 mm.

DIAGNOSIS. — Rostral spine triangular, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with 1 (rarely 2) distinct spine. Median cardiac region with 3 median well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 about twice longer than broad with distomesial spine slightly mucronated, reaching or slightly exceeding antennal peduncle, distolateral spine nearly reaching end of segment 3; segment 3 as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 9 times as long as wide, and less than 1.5 times dactylus length.

REMARKS. — *Paramunida proxima* is closely related to *P. belone* Macpherson, 1993, from New Caledonia, Loyalty Islands, Vanuatu, Tonga, Fiji, Wallis and Futuna. Both species are easily differenciated by the number of striae on the thoracic sternites: with numerous striae on the sternites 4-7 in *P. proxima*, whereas these striae are scarce and only present on the sternite 4 in *P. belone*. Furthermore, the distomesial spine of the antennal segment 2 clearly overreaches the antennal peduncle in *P. belone*, whereas this spine only reaches or slightly exceeds the antennal peduncle in *P. proxima*. The genetic divergences between both species were 5.53% (16S rRNA) and 10.94% (ND1).

P. proxima also resembles *P. leptotes* Macpherson & Baba, 2009, from Japan and Taiwan. The two species can be easily distinguished by the following aspects: the distomesial spine of the antennal segment 2 is long, and clearly exceeds the antennal peduncle by the length of the segment 3 in *P. leptotes*, whereas this spine terminates in the distal end of the peduncle in *P. proxima*; the antennal segment 3 in *P. leptotes* is more elongate, being 1.5–1.7

times longer than wide instead of being as long as in *P. proxima.* The genetic divergences between *P. leptotes* and *P. proxima* were 5.27% (16S rRNA) and 11.06% (ND1).

Genetically the closest relative is *P. polita* Macpherson, 1993 from Indonesia and Philippines. Both species can be easily distinguished by the length of the distomesial spine of the antennal segment 2 which clearly exceeds the antennal peduncle in *P. leptotes*, whereas this spine at most slightly exceeds the antennal peduncle in *P. polita*. The genetic divergences between *P. leptotes* and *P. polita* were 3.84% (16S rRNA) and 12.81% (ND1).

Finally, *P. proxima* can also be related with *P. stichas* Macpherson, 1993 from Solomon Islands, Vanuatu, New Caledonia, Fiji, Field Bank, Wallis Islands, and Bayonnaise Bank (see below under the Remarks of *P. stichas*).

DISTRIBUTION. — Philippines, off Zamboanga, Mindanao, N of the Admiralty Islands, and Indonesia, Kei Islands, Solomon Islands and Vanuatu, between 135 and 402 m

Paramunida salai Cabezas, Macpherson & Machordom, 2009

Figs. 15A, 18C

Paramunida salai Cabezas *et al.*, 2009: 480, fig. 7 (Solomon Islands, 135-325 m).

MATERIAL EXAMINED. — Solomon Islands. SALOMON 1, Stn 1831, 10°12.1'S, 161°19.2'E, 05 October 2001, 135–325 m: 93 M 6.4-11.5 mm, 49 ov. F 8.2-10.7 mm, 1 ov. F 8.6 mm (holotype, MNHN-Ga6517), 21 F 6.7-8.8 mm (paratypes, MNHNGa-6516). — Stn 1834, 10º12.2’S, 161º17.8’E, 05 October 2001, 225-281 m: 2 ov. F 8.8-9.0 mm (paratypes, MNHN-Ga6518).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with median row of 3 well developed spines. Median cardiac region with 3 median well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short striae on sternite 4, and few lateral short striae on sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 about twice longer than broad with distomesial spine mucronated, exceeding antennal peduncle, distolateral spine exceeding end of segment 3; segment 3 nearly twice longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 10 times as long as wide, and 1.2-1.4 times dactylus length.

REMARKS. — *Paramunida salai* belongs to the group of species with the rostral spine longer than the supraocular spines and the distomesial spine of antennal segment 2 mucronated. The closest relative is *P. belone* from New Caledonia, Loyalty Islands, Vanuatu, Tonga, Fiji, Walis and Futuna.

The two species can be distinguished by the number of distinct mesogastric spines, with one (rarely 2) in *P. belone* and 3 or 4 spines, first thicker than others, in *P. salai*. Furthermore, the distomesial spine of the antennal segment 2 clearly exceeds the end of the antennal peduncle and reaches or slightly overreaches the basal segment of the antennular peduncle in *P. belone*; whereas this spine only slightly overreaches the end of the antennal peduncle and clearly not reach the end of the basal segment of the antennular peduncle in *P. salai* (Cabezas *et al.*, 2009).

The genetic divergences between *P. belone* and *P. salai* were 1.30% (16S rRNA) and

3.87% (ND1), respectively.

DISTRIBUTION. — Solomon Islands, between 135 and 325 m.

Paramunida scabra (Henderson, 1885)

Figs. 15B, 18D

Munida scabra Henderson, 1885: 409 (off the Kei Islands, 236 m). — Henderson, 1888: 134, pl. 15, figs 4, 4a, 4b (off Little Kei Islands, 256 m). — Yokoya, 1933: 63 (S of Inuboe-zaki, Sagami Bay, E of Miyazaki, W of Muroto-zaki, Bungo Strait, vicinity of Goto I., E of Chejudo, S of Tsushima, 106–393 m). — Yanagita, 1943: 30, figs 9, 10 (off Miya, Aichi Prefecture, 360 m). — Miyake & Baba, 1967: 242, fig. 13 (East China Sea, 100–158 m). — Baba, 1969: 49 (East China Sea, 310 m). — Kim, 1973: 178 (no record). — Miyake, 1982: 149, pl. 50, fig. 2 (E of Koshiki-jima, Kagoshima, 300–350 m). — Baba in Baba *et al.*, 1986: 175, 292, fig. 125 (Okinawa Trough and Tosa Bay, 150–550 m).

Paramunida scabra. — Baba, 1988: 180 (off NE Borneo, Balabac Strait off N Borneo, Sulu Archipelago, off N Mindanao, off Pacific coast of S Luzon, South China Sea off SW Luzon, off Hong Kong and off SW Formosa, 70–1630 m). — Baba, 1990: fig. 15a (reexamination of type material). — Macpherson, 1993: 462, fig. 8 (in part, Philippines and Indonesia, 143–1075 m). — Baba, 1994: 19 (off Central Queensland, 497–503 m). — Komai, 2000: 360 (list). — Davie, 2002: 66 (no record). — Baba, 2005: 199, 303 (key, synonymies, Japan and Kei Islands, 180–325 m). — Baba *et al.*, 2008: 174 (list of occurrences). — Baba *et al.*, 2009: 281, figs. 257-258 (Taiwan, 520-640 m).

Not *Paramunida scabra*. — Wu *et al.*, 1998: 145, figs 41, 42G (Taiwan) — Macpherson, 1993: 462 (in part) (= *P. tricarinata* (Alcock, 1894)).

Dubious identity:

Munida scabra var. *longipes* Borradaile, 1900: 422 (type locality: Talili Bay, New Britain Talili Bay, New Britain; 3 syntypes not located).

Paramunida scabra Tirmizi & Javed, 1993: 131, figs 58, 59 (off Tanzania and off Mozambique, 100–347 m).

MATERIAL EXAMINED. — Taiwan. Dasi fishing port, Yilan County, 03 December 1984: 1 ov. F 10.8 mm. — 09 November 1995, 1 M 8.0 mm. — Stn CP120, 24º51.79’N, 122º02.54’E, 31 July 2001, 520-640 m: 1 M 5.2 mm (NTOU).

Philippines. PANGLAO. Stn CP2343, 09º26.6’N, 123º51.3’E, 23 May 2005, 309-356 m: 7 M 10.4-12.2 mm, 2 ov. F 11.2-11.8 mm.

Indonesia. Kei Islands. KARUBAR. Stn DW49, 08°00'S, 132°59'E, 29 October 1991, 206-210 m: 1 M 11.9 mm. — Stn CP82, 09°32'S, 131°02'E, 04 November 1991, 215-219 m: 2 M 9.8-10.6 mm, 1 ov. F 12.2 mm, 3 F 10.9-11.7 mm. — Stn 86, 09°26'S, 131°13'E, 04 November 1991, 223-225 m: 3 M 8.5-10.4 mm, 1 ov. F 11.0 mm, 2 F 9.7-10.0 mm (MNHN-Ga 3454).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with a median well developed spine. Median cardiac region with 3 median well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation

of segment 1 spiniform; segment 2 nearly twice longer than broad with distomesial spine spiniform, exceeding segment 3, distolateral spine not reaching end of segment 3; segment 3 about 1.5 times longer than broad Base of P1 carpus without bundle of setae. P2 propodus about 8 times as long as wide, and 1.2-1.4 times dactylus length.

REMARKS. —

Paramunida scabra is closely related to *P. cristata* Macpherson, 2004, from Fiji, Vanuatu, and Taiwan. The two species differ in several constant characters. The longitudinal carina on the rostral spine is clearly thicker in *P. cristata* than in *P. scabra*. Furthermore, the distomesial spine of the antennal segment 2 slightly overreaches the antennal peduncle in *P. cristata*, whereas this spine only exceeds the segment 3 in *P. scabra*. The genetic divergences between the two species were 4.45% (16S rRNA) and 13.33% (ND1).

Paramunida scabra also resembles *P. mozambica* n. sp. from Mozambique. They differ in the following aspects:

— The mesogastric region has 1 (rarely 2) spine in *P. scabra*, whereas there is a row of 3-4 distinct spines in *P. mozambica*.

— The sternal plastron has numerous striae on the sternites 4-7 in *P. scabra*, whereas the sternites 5-7 have few striae on each side in *P. mozambica*.

The genetic divergences between *P. scabra* and *P. mozambica* were 5.49% (16S rRNA) and 9.05% (ND1).

Paramunida scabra (Henderson, 1885) also resembles *P. crinita* n. sp. from the Philippines. The two species can be differentiated by the presence of numerous tuffs of long and dense setae along the anterior branch of the cervical groove in *P. crinita*, whereas these tuffs are absent in *P. scabra*. The genetic divergences between *P. crinita* and *P. scabra* were 7.72% (16S rRNA) and 10.23% (ND1).

Finally, *P. scabra* is also related to *P. evexa* Macpherson, 1993, from Indonesia. Both species can be easily distinguished by the distomesial spine of the antennal segment 2 which is spiniform in *P. scabra* and blunty produced in *P. evexa* (see also Macpherson, 1993). The genetic divergences between *P. evexa* and *P. scabra* were 3.21% (16S rRNA) and 8.26% (ND1).

DISTRIBUTION. —Hong Kong, East and South China Sea (Dongsha), Indonesia, Philippines, Taiwan, Japan, and Australia (off Central Queensland), between 70 and1630 m. The occurrences along the Eastern Africa (off Tanzania and off Mozambique) should be revised.

Paramunida setigera **Baba, 1988**

Figs. 15C, 18E

Paramunida setigera Baba, 1988: 181, figs 74, 75 (Balabac Strait off N Borneo, Davao Gulf off SE Mindanao, Illana Bay off SW Mindanao, between Cebu and Leyte, E coast of Mindoro, South China Sea off SW Luzon, vicinity of Marinduque off SW Luzon, 183–289 m). — Macpherson, 1993: 464 (in part, only specimens from Philippines and Indonesia). — Komai, 2000: 360 (list). —Baba, 2005: 200, 303 (key, synonymies, Bali Sea, 200 m). — Baba *et al.*, 2008: 174 (list of occurrences).

Not *Paramunida setigera* Macpherson, 1993: 464 (in part, specimens from New Caledonia). — Macpherson, 2004: 289 (Fiji, 210–527 m) (= *Paramunida tenera* n. sp.).

MATERIAL EXAMINED. — Philippines. MUSORSTOM1. Stn 20, 13°59'N, 120°20'E, 20 March 1976, 208-222 m: 1 M 7.3 mm, 1 ov. F 8.6 mm. — Stn 51, 13°49'N, 120°04'E, 25 March 1976, 170-200 m: 1 M 9.4 mm, 2 ov. F 8.4-8.5 mm.
MUSORSTOM 3. Stn 139, 11°53'S, 122°15'E, 06 June 1985, 240-267 m: 3 M 10.3-11.3 mm, 1 ov. F 10.4 mm.
PANGLAO. Stn CP2332, 09º41.214'N, 123º47.32'E, 22 May 2005, 270-396 m: 10 M 9.5-11.7 mm, 11 ov. F 9.4-10.5 mm, 1 F 7.8 mm. — Stn CP2340, 09º30.8'N, 123º46.3'E, 23 May 2005, 231-271 m: 6 M 7.5-12.1 mm, 7 ov. F 9.7-11.8 mm, 7 F 5.6-10.4 mm. — Stn CP2381, 08º41.2'N, 123º18'E, 28 May 2005, 241-259 m: 2 M 9.0-10.9 mm, 12 ov. F 9.0-10.6 mm, 1 F 9.4 mm.
Indonesia. CORINDON. Stn CH273, 01º56.0'S, 119º16.0'E, 07 November 1980, 180-220 m: 3 M 9.5-9.7 mm, 4 ov. F 7.9-9.0 mm, 4 F 5.6-8.4 mm (MNHN-Ga 3463). KARUBAR. Stn CP66, 09°01'S, 132°09'E, 01 November 1991, 211-217 m: 3 M 8.1-9.5 mm. — Stn CP79, 09°16'S, 131°22'E, 03 November 1991, 239-250 m: 4 M 10.2-11.3 mm (MNHN-Ga 3468).

DIAGNOSIS. — Rostral spine spiniform, smaller than supraocular spines, with thin dorsal carina; with row of small epigastric spines behind rostral spine; margin between rostral and supraocular spines straight. Mesogastric and cardiac regions without well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 more than twice longer than broad with distomesial spine spiniform, exceeding antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 twice longer than broad. Base of P1 carpus with bundle of setae. P2 propodus about 12-14 times as long as wide, and 1.3-1.4 times dactylus length.

REMARKS. — *Paramunida setigera* is closely related to *P. curvata* Macpherson, 2004, from Fiji and Vanuatu. The two species can be easily differentiated by the shape of the rostrum, being the margin between the rostral and supraocular spines convex in *P. curvata*, whereas this margin is straight or slightly concave in *P. setigera*. The genetic divergences were 9.57% (16S rRNA) and 13.37% (ND1).

The species is also related to *P. tenera* n. sp. from Fiji, Vanuatu and New Caledonia (see below under the Remarks of that species).

DISTRIBUTION. — Philippines and Indonesia, between 170 and 289 m.

Paramunida spatula Macpherson, 2006

Fig. 18F

Paramunida spatula Macpherson, 2006: 325, fig. 16. — Baba *et al.*, 2008: 174.

MATERIAL EXAMINED. — French Polynesia. Austral Archipelago. BENTHAUS, Stn DW1897, 27º34.27´S, 144º26.68´W, 08 November 2002, 480–700 m: 1 M 9.4 mm (MNHN Ga 5292).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; with row of small epigastric spines behind rostral spine; margin between rostral and

supraocular spines straight. Mesogastric region with row of 3 well developed spines. Cardiac region with 3 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short striae on sternite 4, and few short striae on each side of sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spatulate; segment 2 slightly longer than broad with distomesial spine of segment 2 spiniform, reaching midlength of segment 3, distolateral spine nearly reaching end of segment 3; segment 3 1.5 times longer than broad. P2 propodus about 15 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida spatula* is easily differentiated from the other species of the genus by the shape of the anterior prolongation of the antennal segment 1, being spatulate in *P. spatula* and spiniform in the other species.

DISTRIBUTION. — French Polynesia. Austral Archipelago, between 480 and 700 m.

Paramunida spica n.sp.
Figs. 10, 15D

Paramunida stichas Macpherson, 1993: 465 (in part, only specimens from Indonesia).

TYPE MATERIAL. — *Holotype*: Vanuatu. SANTO, Stn AT34, 15°35.9'S, 167°17.1'E, 26 September 2006, 234-270 m: ov. F 7.1 mm (MNHN-Gaxxxx).
Paratypes: Vanuatu. SANTO, Stn AT34, 15°35.9'S, 167°17.1'E, 26 September 2006, 234-270 m: 4 M 5.9-7.8 mm, 7 ov. F 6.2-8.6 mm.
Indonesia. Kei Islands. KARUBAR. Stn DW15, 05°17'S, 132°41'E, 24 October 1991, 212-221 m: 1 M 11.9 mm, 1 F 10.0 mm (MNHN-Gaxxxx).

ETYMOLOGY. — The name *spica* refers to one of the stars from the southern hemisphere (constellation of Virgo).

DESCRIPTION. — *Carapace*: As long as broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with few short unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; with median row of small spines behind rostral spine. Mesogastric region with row of 3-4 spines. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3-4 moderated-sized spines, first thicker than others. Each branchial region with row of spines near cardiac region. Frontal margin slightly concave. Some spines and iridescent setae on anterior half of frontal margin. Anterolateral spine small, nearly reaching sinus between rostral and supraocular spines. Rostral spine triangular, with thin dorsal longitudinal carina; supraocular spines well developed and as long and more slender than rostrum (Figs. 10A, 10B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-7 smooth (Fig. 10C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 small spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 10A).

Eyes: Maximum corneal diameter about one-third distance between bases of anterolateral spines.

Antennule: Segment 1 exceeding corneae, with distomesial spine small and slightly shorter than distolateral; about three times longer than wide and with fringe of long setae along lateral margin; Lateral margin of antennular segment 1 with straight (distal) portion as long as convex (proximal) portion. Flagelum segments 1 and 2 slender and not squamate, first segment slightly longer than second (Fig. 10D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-fourth of its length. Segment 2 about twice length of segment 3 and twice longer (measured along lateral margin) than wide (measured at midlength of segment), ventral surface with scales; distomesial spine mucronated and without tuff of setae at base, overreaching antennal peduncle, overreaching mid-length of anterior prolongation of segment 1, although not reaching end of basal antennular segment 1 (excluding distal spines), distolateral spine nearly reaching midlenght of segment 3; segment 3 nearly twice longer than wide and unarmed (Fig. 10D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing one spine; merus with median small spine on flexor margin; extensor margin unarmed (Fig. 10E).

Pereopod 1 (cheliped): Long and slender, squamate, between 4.5-6.3 times carapace length; carpus 0.9-1.0 times palm length, and 7-11 times longer than height; palm 1.4-1.8 times fingers length. Base of carpus without bundle of setae (Fig. 10F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 3.2-3.5 times carapace length, merus 1.3-1.4 times longer than carapace, about 12-15 times as long as high, 3.8-4.6 times as long as carpus and 1.7 times as long as propodus; propodus about 9-11 times as long as high, and 1.1-1.3 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, small distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus clearly not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus slightly longer than P2 merus; propodus and dactylus slightly longer than those of P2. P4 slightly longer than P2; merus about 1.3-1.5 times carapace length; propodus and dactylus slightly longer than those of P3; merocarpal articulation slightly exceeding end of anterior prolongation of segmetn 1 of antennal peduncle (Fig. 10G, 10H, 10I).

REMARKS. — The new species is closely similar to *P. belone* Macpherson, 1993, from New Caledonia, Loyalty Islands, Vanuatu, Tonga, Fiji, Walis and Futuna. The two species can be easily differentiated by the following characters. The mesogastric region has only one (rarely 2) distinct spine in *P. belone*, whereas there is a row of 3-4 moderated-sized spines in *P. spica*; the lateral margin of the antennular segment 1 has the convex (proximal) portion as long as the straight (distal) portion in *P. spica*; whereas this proximal portion is clearly longer than the distal portion in *P. belone*. The genetic divergences between *P. belone* and *P. spica* were 4.26% (16S rRNA) and 10.85% (ND1).

DISTRIBUTION. — Vanuatu, between 234 and 270 m.

Paramunida stichas Macpherson, 1993

Figs. 15E, 18G

Paramunida stichas Macpherson, 1993: 465, figs 9, 15 (in part, New Caledonia and Fiji, 210–590 m). — Macpherson, 1996: 417 (SW Pacific (Field Bank, Wallis Islands, and Bayonnaise Bank), 400–430 m). — Macpherson, 2004: 290 (Fiji and Tonga, 371–591 m). — Baba, 2005: 304 (key, synonymies). — Poore *et al.*, 2008: 22 (SW Australia, 388–404 m). — Baba *et al.*, 2008: 174 (list of occurrences).

Not *Paramunida stichas* Macpherson, 1993: 465 (in part, specimens from Indonesia) (= *P. spica* n. sp.).

MATERIAL EXAMINED. — New Caledonia. MUSORSTOM 4. Stn 170, 18°57.00'S, 163°12.60'E, 17 September 1985, 485 m: 1 M 10.4 mm, 4 ov. F 8.3-11.2 mm. HALIPRO 1. Stn CP877, 23°03.51'S, 166°59.20'E, 31 March 1994, 464-480 m: 1 M 8.7 mm, 3 ov. F 9.8-11.0 mm. NORFOLK 1. Stn DW1694, 24°40'S, 168°39'E, 24 June 2001, 575-589 m: 1 ov. F 8.6 mm.

Vanuatu. MUSORSTOM 8. Stn CP974, 19°21.51'S, 169°28.26'E, 22 September 1994, 492-520 m: 5 M 7.8-12.6 mm, 1 ov. F 8.6 mm, 1 F 11.3 mm. SANTO. Stn AT11, 15°39.5'S, 167°01.5'E, 17 September 2006, 272-286 m: 1 M 12.5 mm.

Solomon Islands. SALOMON 1. Stn CP1831, 10°12.1'S, 161°19.2'E, 05 October 2001, 135-325 m: 4 M 8.4-12.6 mm, 2 ov. F 8.1-9.6 mm, 2 F 9.4-10.5 mm.

Tonga Islands. BORDAU 2. Stn CP1510, 21°04.65'S, 175°22.52'W, 31 May 2000, 461-497 m: 2 M 9.2-12.7 mm, 3 ov. F 10.9-12.1 mm.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with row of 3 well developed spines. Cardiac region with 3 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with some short striae on sternite 4, and few short striae on each side of sternites 5-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 slightly longer than broad with distomesial spine mucronated, clearly overreaching segment 3, distolateral spine nearly reaching end of segment 3; segment 3 1.5 times longer than broad. Base of P1 carpus without bundle of setae P2 propodus about 15 times as long as wide, and 1.5 times dactylus length.

REMARKS. — *Paramunida stichas* belongs to the group of species with the rostral spine longer than the supraocular spines, and with the distomesial spine of antennal segment 2 mucronated. The species is closely related to *P. proxima* (Henderson, 1885), from Philippines, off Zamboanga, Mindanao, N of the Admiralty Islands, Indonesia, Kei Islands, Solomon Islands, and Vanuatu. Both species can be differentiated by the number of spines in the mesogastric region: a row of 3 well developed spines in *P. stichas*, whereas there is only 1 (rarely 2) well developed spine in *P. proxima*.

Genetically the divergences among *P. stichas* and *P. proxima* were 2.87% (16S rRNA) and 6.47% (ND1).

DISTRIBUTION. — Solomon Islands, Vanuatu, New Caledonia, Fiji, Field Bank, Wallis Islands, Bayonnaise Bank and, SW Australia between 135 and 591 m.

Paramunida tenera n.sp.
Figs. 11, 15F

Paramunida setigera Macpherson, 1993: 464 (in part, specimens from New Caledonia). — Macpherson, 2004: 289 (Fiji, 210–527 m).

TYPE MATERIAL. — *Holotype*: New Caledonia. BATHUS 4. Stn CP946, 20°33' S, 164°58' E, 10 August 1944, 386-430 m: M 8.0 mm (MNHN-Gaxxxx).

Paratypes: Fiji. MUSORSTOM 10. Stn CP1349, 17°31.07''S, 178°38,79'E, 11 August 1998, 244-252 m: 6 M 7.4-9.3 mm, 5 ov. F 7.8-8.5 mm, 6 F 5.7-9.2 mm (MNHN-Gaxxxx).

Vanuatu. BOA 0. Stn CP2326,15º39.83'S, 167º01.9'E, 18 November 2004, 260-313 m: 1 M 9.3-9.4 mm, 3 ov. F 7.7-8.9 mm (MNHN-Gaxxxx). — Stn CP2327, 15º39.48'S, 167º01.46'E, 18 November 2004, 287-440 m: 18 M 8.5-11.7 mm, 15 ov. F 8.2-10.5 mm (MNHN-Gaxxxx) (one incompete male, *P*. aff. *setigera*, could be a different species). SANTO. Stn AT1, 15°33.8'S, 167°19.5'E, 14 September 2006, 167-367 m: 1 F 8.2 mm (MNHN-Gaxxxx). — Stn AT2, 15°32.8'S, 167°16.5'E, 14 September 2006, 160-175 m: 1 ov. F 7.5 mm (MNHN-Gaxxxx). — Stn AT 19, 15°40.8'S, 167°00.5'E, 21 September 2006, 503-600 m: 1 ov. F 8.0 mm (MNHN-Gaxxxx). — Stn AT27, 15°22.4'S, 167°15.4'E, 23 September 2006, 341-347 m: 1 M 9.6 mm (MNHN-Gaxxxx).

New Caledonia. BATHUS 4. Stn CP946, 20°33' S, 164°58' E, 10 August 1944, 386-430 m: 4 M 7.9-12.2 mm, 1 ov. F 9.5 mm, 1 F 10.2 mm (MNHN-Gaxxxx).

ETYMOLOGY. — From the Latin, *tener*, delicate, in reference to the thin and long walking legs.

DESCRIPTION. — *Carapace*: Slightly longer than broad. Dorsal surface covered with numerous spinules; each spinule usually on short arcuate striae, with some unirramous setae. Epigastric region with 2 spines, each behind supraocular spine; withouth median row of spines behind rostral spine. Mesogastric region without row of median spines. Cervical groove distinct. Cardiac and anterior branchial regions slightly circumscribed. Cardiac region with a median row of 3 well developed spines, first thicker than others. Each branchial region with 1-2 moderate- sized spines near cardiac region. Frontal margin slightly concave. Lateral margins convex, with some spines and iridescent setae on anterior half. Anterolateral spine well developed, reaching sinus between rostral and supraocular spines. Rostral spine short, triangular and with thin dorsal longitudinal carina; supraocular spines well developed and longer or as long as rostral spine (Figs. 11A, 11B).

Sternum: Thoracic sternite 4 with few arcuate striae; sternites 5-7 with few and small striae on lateral sides (Fig. 11C).

Abdomen: Abdominal somites 2-3 each with 4 well-developed spines on anterior ridge, posterior ridge with 2 median spines. Abdominal somite 4 with 4 spines on anterior ridge; posterior ridge with distinct single median spine. Ridges with numerous spinules and a few small spines (Fig. 11A).

Eyes: Maximum corneal diameter more than one-third distance between bases of anterolateral spines.

Antennule: Segment 1 reaching or slightly exceeding corneae, with distomesial spine small and shorter than distolateral; twice longer than wide and with fringe of long setae along lateral margin; lateral margin with straight (distal) portion clearly shorter than convex (proximal) portion. Flagelum segments 1 and 2 slender and smooth or with denticulated fine in second segment, first segment longer than second (Fig. 11D).

Antenna: Anterior prolongation of segment 1 clearly overreaching antennular peduncle by about one-third of its length. Segment 2 about 1.5 times length of segment 3 and about twice longer (measured along lateral margin) than wide (measured at midlength of segment), ventral surface with scales; distomesial spine mucronated with no tuff of setae at base, overreaching antennal peduncle, overreaching mid-length of anterior prolongation of segment 1, although not reaching end of basal segment of antennule (excluding distal spines), distolateral spine reaching midlength of segment 3; segment 3 nearly twice longer than wide and unarmed (Fig. 11D).

Maxilliped 3: Ischium about twice length of merus measured along dorsal margin, distoventrally bearing long spine; merus with median well developed spine on flexor margin; extensor margin unarmed (Fig. 11E).

Pereopod 1 (cheliped): Long and slender, squamate, between 6.7-7.1 times carapace length; carpus 0.8 times palm length, and 9.1-11.0 times longer than height; palm 1.4-1.6 times fingers length. Base of carpus without bundle of setae (Fig. 11F).

Pereopods 2-4: Long and slender, with numerous scales on lateral sides of meri, carpi and propodi; scales with short setae. P2 4.1-4.8 times carapace length, merus 1.8-2.1 times longer than carapace, about 17-20 times as long as high, 4.2-4.6 times as long as carpus and 1.7-1.8 times as long as propodus; propodus about 13-15 times as long as high, and 1.2-1.5 times dactylus length. Merus with well developed spines on dorsal border, increasing in size distally, ventral margin with few spines and one well developed distal spine; row of small spines along ventrolateral margin. Carpus with some small dorsal spines, well developed distal spine on dorsal and ventral margin. Propodus with small movable ventral spines. Dactylus compressed, slightly curved, with longitudinal carinae along mesial and lateral sides, ventral border unarmed. End of P2 carpus clearly not reaching end of P1 merus. P3 with similar spination and segment proportions than P2; merus as long as P2 merus; propodus and dactylus slightly longer than those of P2. P4 slightly longer than P2; merus about 2.0-2.2 times carapace length; propodus and dactylus slightly longer than those of P3; merocarpal articulation clearly exceeding end of anterior prolongation of segment 1 of antennal peduncle (Fig. 11G, 11H, 11I).

REMARKS. — The new species is closely related to *P. setigera* Baba, 1988, from the Philippines and Indonesia. Both species can be differentiated by the following characters:
— The thoracic sternites have numerous striae in *P. setigera*, whereas there are few striae in sternites 4-7 on the new species.
— A bundle of setae is present at base of the P1 carpus in *P. setigera,* whereas it is absent in the new species.

Genetically the divergences between *P. tenera* and *P. setigera* were 4.85% (16S rRNA) and 9.15% (ND1).

One incomplete male from BOA 0, Stn CP2327 (*P. aff. setigera*), showed a significant genetic divergence with the other specimens, 4.71% (16S rRNA) and 8.90% (ND1), suggesting the existence of an additional cryptic species. Unfortunately, the incomplete specimen avoids a complete description, and additional material is necessary in order to determine its taxonomic status.

DISTRIBUTION. — Fiji, Vanuatu and New Caledonia, between 160 and 600 m.

Paramunida thalie Macpherson, 1993

Figs. 15G, 18H

Paramunida thalie Macpherson, 1993: 467, figs 10, 16 (Loyalty Islands, 245–283 m). — Macpherson, 2004: 290 (Fiji, 310–420 m). — Ahyong & Poore, 2004: 68 (Queensland, 210 m). — Baba, 2005: 304 (key, synonymies). — Baba *et al.*, 2008: 175 (list of occurrences).

MATERIAL EXAMINED. — Vanuatu. MUSORSTOM 8. Stn CP971, 20°19'S, 169°53'E, 21 September 1994, 250-315 m:1 M 11.5 mm, 1 ov. F 10.9 mm.
New Caledonia. BIOCAL. Stn CP110, 22°12.38'S, 167°06.43'E, 9 September 1985, 275 m: 5 M 7.3-10.7 mm, 3 F 7.0-9.3 mm.
Chesterfield Islands. EBISCO. Stn CP2632, 21º03.655'S, 160º44.673'E, 21 May 2005, 297-378 m:1 M 8.8 mm.

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with row of 3 well developed spines. Cardiac region with 3 well developed spines. Few and short setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of segment 1 spiniform; segment 2 slightly longer than broad with distomesial spine spiniform, exceeding segment 3, distolateral spine not reaching end of segment 3; segment 3 twice as long as broad. Base of P1 carpus without bundle of setae. P2 propodus about 9 times as long as wide, and 1.2-1.4 times dactylus length.

REMARKS. — *Paramunida thalie* is closely related to *P. amphitrita* Macpherson, 1996, from Futuna, Fiji, Tonga and New Caledonia islands. They can be easily distinguished by the presence of numerous arcuate striae in the thoracic sternites 5-7 of *P. thalie,* whereas these sternites are smooth in *P. amphitrita*. The two species can also be differentiated by the length of the P2-4 propodi and the length of the distomesial spine of the antennal segment 2 (see Macpherson, 1996). The genetic divergences between *P. amphitrita* and *P. thalie* were 4.70% (16S rRNA) and 11.16% (ND1).

DISTRIBUTION. — Vanuatu, New Caledonia, Loyalty Islands, Chesterfield Islands, Fiji and Queensland, between 245 and 420 m.

Paramunida tricarinata (Alcock, 1894)

Figs. 15H, 18I

Munida tricarinata Alcock, 1894: 324 (Andaman Sea, 205 m). — Alcock, 1901: 246 (Andaman Sea and Arabian Sea off N. Maldive Atoll, 205–384 m). — Alcock & Anderson, 1895: pl. 12, fig. 1 (no record).
Paramunida tricarinata. — Baba, 2005: 304 (key, synonymies). — Baba *et al.*, 2008: 175 (list of occurrences). — Baba *et al.*, 2009: 283, figs. 260-261 (Taiwan).
Paramunida scabra. — Wu *et al.*, 1998: 145, figs 41, 42G (Taiwan). — Macpherson, 1993: 462 (in part) (not *P. scabra* (Henderson, 1885)).

Dubious identity:

Munida tricarinata Laurie, 1926: 138 (Providence and Saya De Malha Bank, 281–275 m). — Tirmizi, 1966: 202, fig. 21 (Zanzibar and Maldives, 183–457 m).

Paramunida tricarinata. — Baba, 1990: 968, fig. 15b (Madagascar, 308–444 m). — Macpherson, 1993: 469, fig. 11 (Maldives Islands and Madagascar, 238–428 m).

MATERIAL EXAMINED. — Taiwan. Dashi fishing port (no depth recorded), Yilan County, 05 August 1982: 1 M 8.0 mm. — 09 September 1989: 1 ov. F 7.0 mm, 2 F 8.3-8.5 mm. —03 March 1991: 1 M 8.4 mm, 2 ov. F 7.9-8.1 mm, 1 F 5.2 mm. — 19 April 1995: 1 M 9.1 mm, 1 ov. F 9.1 mm. —13 June 1995: 1 M 8.9 mm. — 09 November 1995: 4 M 10.2–12.7 mm, 2 F 10.4-12.7 mm. — 28 January 1997: 1 M 9.6 mm. — 01 September 1997: 1 ov. F 9.8 mm. — 23 September 1997: 1 M 9.8 mm, 1 ov. F 9.5 mm. — 30 October 1997: 1 ov. F 10.1 mm. — 18 November 1997: 1 M 8.6 mm. — 05 December 1997: 1 M 10.1 mm, 1 ov. F 8.9 mm. — 26 January 1999: 1 M 9.0 mm. — 23 March 1999: 1 M 9.8 mm. — 09 December 2003: 1 F 11.5 mm. — 16 December 2004: 6 M 10.8–11.6 mm, 1 ov. F 11.4 mm.

Philippines. MUSORSTOM 2. Stn 31, 13°40'N, 120°54'E, 24 November 1980, 204-230 m: 5 M 8.7-11.6 mm, 2 ov. F 8.5-9.0 mm (MNHN-Ga 3430). — Stn 35, 13°28'N, 121°12'E, 160-198 m: 2 M 7.7-9.0 mm, 3 ov. F 9.0-9.6 mm, 1 F 7.3 mm (MNHN-Ga 3431).

DIAGNOSIS. — Rostral spine spiniform, larger than supraocular spines, with thin dorsal carina; margin between rostral and supraocular spines straight. Mesogastric region with row of 3 well developed spines. Cardiac region with 3-4 well developed spines. Tuffs of long and dense setae setae along anterior branch of cervical groove. Sternal plastron with numerous striae on sternites 4-7. Lateral margin of antennular segment 1 with straight (distal) portion clearly shorter than convex (proximal) portion. Antennal peduncle with anterior prolongation of antennal segment 1 spiniform; segment 2 slightly longer than broad, with distomesial spine spiniform, slightly overreaching end of antennal peduncle, distolateral spine not reaching end of segment 3; segment 3 1.4 times longer than broad. Base of P1 carpus without bundle of setae. P2 propodus about 9 times as long as wide, and 1.2-1.4 times dactylus length.

REMARKS. — The occurrences of this species along the eastern coast of Africa and Madagascar (e.g. Laurie, 1926; Tirmizi, 1966; Baba, 1990) should be reviewed and compared with the new species described from Madagascar and Mozambique (*P. marionis* and *P. mozambica*).

Paramunida tricarinata is closely similar to *P. crinita* n. sp., from the Philippines, and *P. ascella* n. sp., from Vanuatu.

P. tricarinata can be differentiated from *P. crinita* by the following characters:

— The mesogastric region has 1 (rarely 2) well developed spine in *P. crinita*, whereas there is a row of 3-4 distinct spines in *P. tricarinata*.

— The distomesial spine of the antennal segment 2 clearly overreaches the antennal peduncle in *P. tricarinata*, whereas this spine never exceeds the end of the antennal peduncle in *P. crinita*.

P. tricarinata is easily distinguished from *P. ascella* by the following aspects:

— The rostral spine is spiniform in *P. tricarinata*, whereas this spine is more triangular in *P. ascella*.

— The distomesial spine of the antennal segment 2 is mucronated in *P. ascella*, whereas this spine is spiniform in *P. tricarinata*. Furthermore, this spine exceeds antennal peduncle in *P. tricarinata*, whereas the spine never overreaches this peduncle in *P. ascella*.

Genetically the divergences among *P. tricarinata* and the other two species were: *P.*

crinita 1.13% (16S rRNA) and 2.06% (ND1), and *P. ascella* 1.41% (16S rRNA) and 2.19% (ND1).

Paramunida tricarinata is also closely related to *P. marionis* n. sp. from Madagascar, and they can be differentiated by the following characters:

— *P. marionis* has a very spiny gastric region with row of spines along the carapace, whereas in *P. tricarinata* there are less spines and smaller in size.

— The distolateral spine of the antennal segment 2 does not reach the end of the antennal segment 3 in *P. tricarinata,* whereas this spine slightly overreaches the end of the third segment in *P. marionis*.

DISTRIBUTION. — Arabian Sea, Maldives Islands, Andaman Sea, Taiwan and Philippines, between 205 and 384 m. The occurrences in other localities require confirmation.

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FIGURE LEGENDS

FIGURE 1. *Paramunida achernar* n. sp. ovigerous female holotype, 9.6 mm (MNHN-Ga xxx). Tonga. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 2. *Paramunida antares* n. sp. male holotype, 9.0 mm (MNHN-Ga xxx). New Caledonia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P2, lateral view. G, right P3, lateral view. H, right P4, lateral view. Scale: 1 mm.

FIGURE 3. *Paramunida ascella* n. sp. male holotype, 10.9 mm (MNHN-Ga xxx). Vanuatu. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 4. *Paramunida crinita* n. sp. male holotype, 7.8 mm (MNHN-Ga xxx). Philippines. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, left P2, lateral view. H, right P3, lateral view. I, left P4, lateral view. Scale: 1 mm.

FIGURE 5. *Paramunida marionis* n. sp. male holotype, 10.7 mm (MNHN-Ga xxx). Madagascar. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P1, lateral view. G, right P2, lateral view. H, left P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 6. *Paramunida microrhina* n. sp. ovigerous female holotype, 5.1 mm (MNHN-Ga xxx). Chesterfield Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 7. *Paramunida mozambica* n. sp. ovigerous female holotype, 6.9 mm (MNHN-Ga xxx). Mozambique. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 8. *Paramunida parvispina* n. sp. ovigerous female holotype, 7.0 mm (MNHN-Ga xxx). Chesterfield Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 9. *Paramunida poorei* n. sp. male holotype, 9.3 mm (MNHN-Ga xxx). French Polynesia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 10. *Paramunida spica* n. sp. ovigerous female holotype, 7.1 mm (MNHN-Ga xxx). Vanuatu. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

FIGURE 11. *Paramunida tenera* n. sp. male holotype, 8.0 mm (MNHN-Ga xxx). New Caledonia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1 merus and carpus, lateral view. G, right P1 palm and fingers. H, right P2, lateral view. I, right P3, lateral view. J, right P4, lateral view. Scale: 1 mm..

FIGURE 12. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida achernar*, holotype, ovigerous female 9.6 mm. B, *Paramunida amphitrita*, LIFOU, Stn DW15, male 10.3 mm. C, *Paramunida antares*, holotype, male 9.0 mm. D, *Paramunida ascella*, holotype, male 10.9 mm. E, *Paramunida belone*, MUSORSTOM 8, Stn CP963, male 12.0 mm. F, *Paramunida cretata*, BORDAU 1, Stn CP1412, ovigerous female 10.9 mm. G, *Paramunida crinita*, holotype, male 7.8 mm. H, *Paramunida cristata*, Taiwan, Stn CP269, female 10.1 mm. I, *Paramunida curvata*, MUSORSTOM 10, Stn CP1389, ovigerous female 8.8 mm.

FIGURE 13. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida echinata*, MUSORSTOM 9, Stn CP963, male 12.0 mm. B, *Paramunida evexa*, KARUBAR, Stn CP86, male 9.1 mm. C, *Paramunida granulata*, MUSORSTOM 8, Stn CP971, male 8.3 mm. D, *Paramunida hawaiiensis*, Hawaii, male 9.3 mm. E, *Paramunida labis*, MUSORSTOM 8, Stn CP1027, male 12.0 mm. F, *Paramunida leptotes*, Taiwan, Stn CD380, holotype, male 10.3 mm. G, *Paramunida longior*, BATHUS, Stn CP742, male 9.4 mm. H, *Paramunida lophia*, SALOMON 2, Stn 2199, male 9.7 mm. I, *Paramunida luminata*, MUSORSTOM 7, Stn 629, male 12.6 mm.

FIGURE 14. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida marionis*, holotype male 10.7 mm. B, *Paramunida microrhina*, holotype ovigerous female 5.1 mm. C, *Paramunida mozambica*, holotype, ovigerous female 6.9 mm. D, *Paramunida parvispina*, holotype, ovigerous female 7.0 mm. E, *Paramunida pictura*, MUSORSTOM 8, Stn CP1025, male 8.7 mm. F, *Paramunida polita*, KARUBAR, Stn CP35, female 12.6 mm. G, *Paramunida poorei*, holotype, male 9.3 mm. H, *Paramunida pronoe*, NORFOLK 1, Stn CP1670, ovigerous female 7.7 mm. I, *Paramunida proxima*, SALOMON 1, Stn CP1831, male 11.8 mm.

FIGURE 15. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida salai*, SALOMON 1, Stn CP1831, male 10.2 mm. B, *Paramunida scabra*, KARUBAR, Stn CP86, male 11.6 mm. C, *Paramunida setigera*, MUSORSTOM 3, Stn 139, ovigerous female 10.6 mm. D, *Paramunida spica*, holotype, ovigerous female 7.1 mm. E, *Paramunida stichas*, HALIPRO 1, Stn Stn CP877, female 8.9 mm. F, *Paramunida tenera*, holotype, male 8.0 mm. G, *Paramunida thalie*, EBISCO, Stn CP2632, male 8.8 mm. H, *Paramunida tricarinata*, MUSORSTOM 2, Stn CP35, ovigerous female 9.8 mm.

FIGURE 16. Left antennule and antenna, ventral view. A, *Paramunida amphitrita*, LIFOU, Stn DW1650, ov. F 10.5 mm. B, *Paramunida antipodes* (from Ahyong & Poore, 2004). C, *Paramunida belone*, MUSORSTOM 8, Stn 963, male 12.0 mm. D, *Paramunida cretata*,

BORDAU 1, Stn CP1412, ovgerous female 10.9 mm. E, *Paramunida cristata*, Taiwan female 10.1 mm. F, *Paramunida curvata*, MUSORSTOM 10, Stn 1390, ovigerous female 10.0 mm. G, *Paramunida echinata*, MUSORSTOM 9, Stn CP1176, male 13.4 mm. H, *Paramunida evexa*, KARUBAR, Stn CP86, male 10.6 mm. I, *Paramunida granulata*, MUSORSTOM 8, Stn CP1027, male 12.4 mm.

FIGURE 17. Left antennule and antenna, ventral view. A, *Paramunida hawaiiensis*, Hawaii, M 9.3 mm. B, *Paramunida labis*, MUSORSTOM 8, Stn CP971, female 8.3 mm. C, *Paramunida leptotes*, Taiwan, ovigerous female 12.8 mm. D, *Paramunida longior*, BATHUS 2, Stn CP742, male 9.6 mm. F, *Paramunida lophia*, SALOMON 2, Stn 2199, male 11.8 mm. G, *Paramunida luminata*, MUSORSTOM 7, Stn 629, male 11.4 mm. H, *Paramunida pictura*, MUSORSTOM 8, Stn 1025, male 9.8 mm. I, *Paramunida polita*, KARUBAR, Stn CP86, male 11.6 mm. Right antenna, ventral view. E, *Paramunida longior*, holotype, 8.5 mm.

FIGURE 18. Left antennule and antenna, ventral view. A, *Paramunida pronoe*, NORFOLK 1, Stn CP1670, ovigerous female 8.3 mm. B, *Paramunida proxima*, SALOMON 1, CP1831, male 11.6 mm. C, *Paramunida salai*, SALOMON 1, Stn CP1831, male 11.0 mm. D, *Paramunida scabra*, KARUBAR, Stn 86, male 10.4 mm. E, *Paramunida setigera*, MUSORSTOM 3, Stn 139, male 10.3 mm. F, *Paramunida spatula*, BENTHAUS, Stn DW1897, holotype, male 9.4 mm (from Macpherson, 2006). G, *Paramunida stichas*, HALIPRO 1, Stn CP877, ovigerous female 11.0 mm. H, *Paramunida thalie*, EBISCO, Stn CP2632, male 8.8 mm. I, *Paramunida tricarinata*, MUSORSTOM 2, Stn 35, male 9.0 mm.

TABLE 1. Divergences (uncorrected “p” distances, per unit) among specimens analyzed: ND1 (above diagonal) and 16S rRNA (below diagonal).

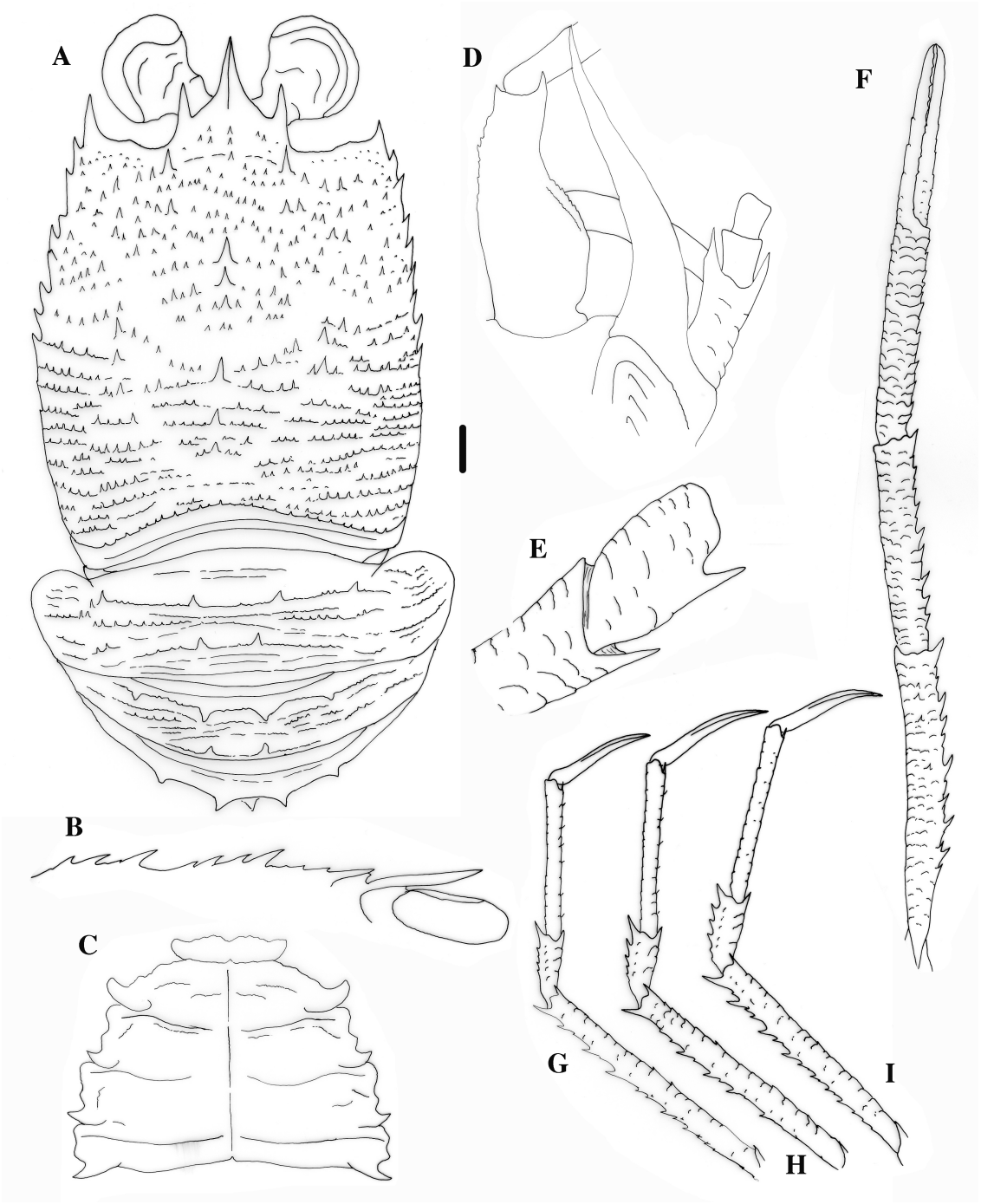


FIGURE 1. *Paramunida achernar* n. sp. ovigerous female holotype, 9.6 mm (MNHN-Ga xxx). Tonga. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

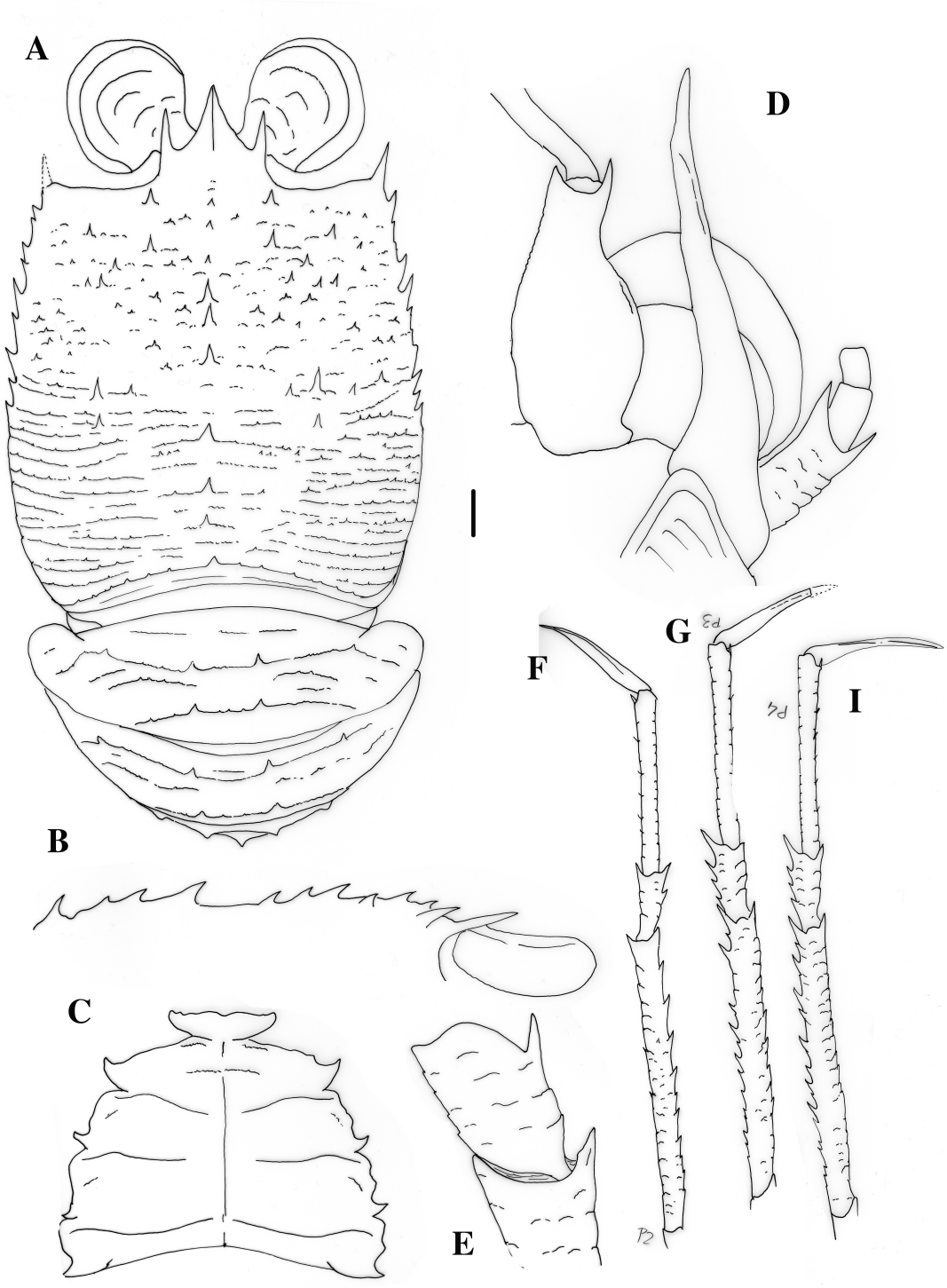


FIGURE 2. *Paramunida antares* n. sp. male holotype, 9.0 mm (MNHN-Ga xxx). New Caledonia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P2, lateral view. G, right P3, lateral view. H, right P4, lateral view. Scale: 1 mm.

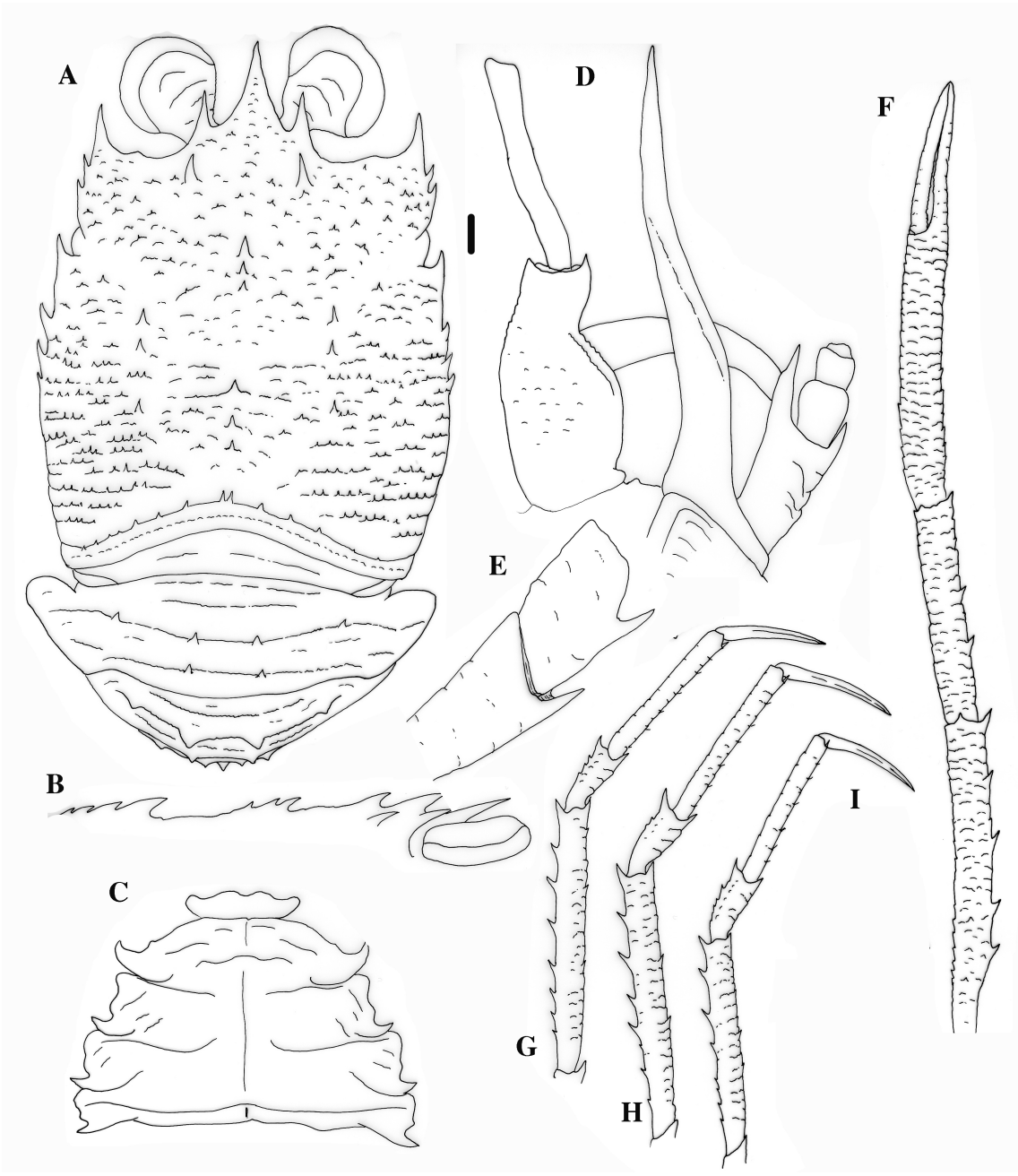


FIGURE 3. *Paramunida ascella* n. sp. male holotype, 10.9 mm (MNHN-Ga xxx). Vanuatu. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

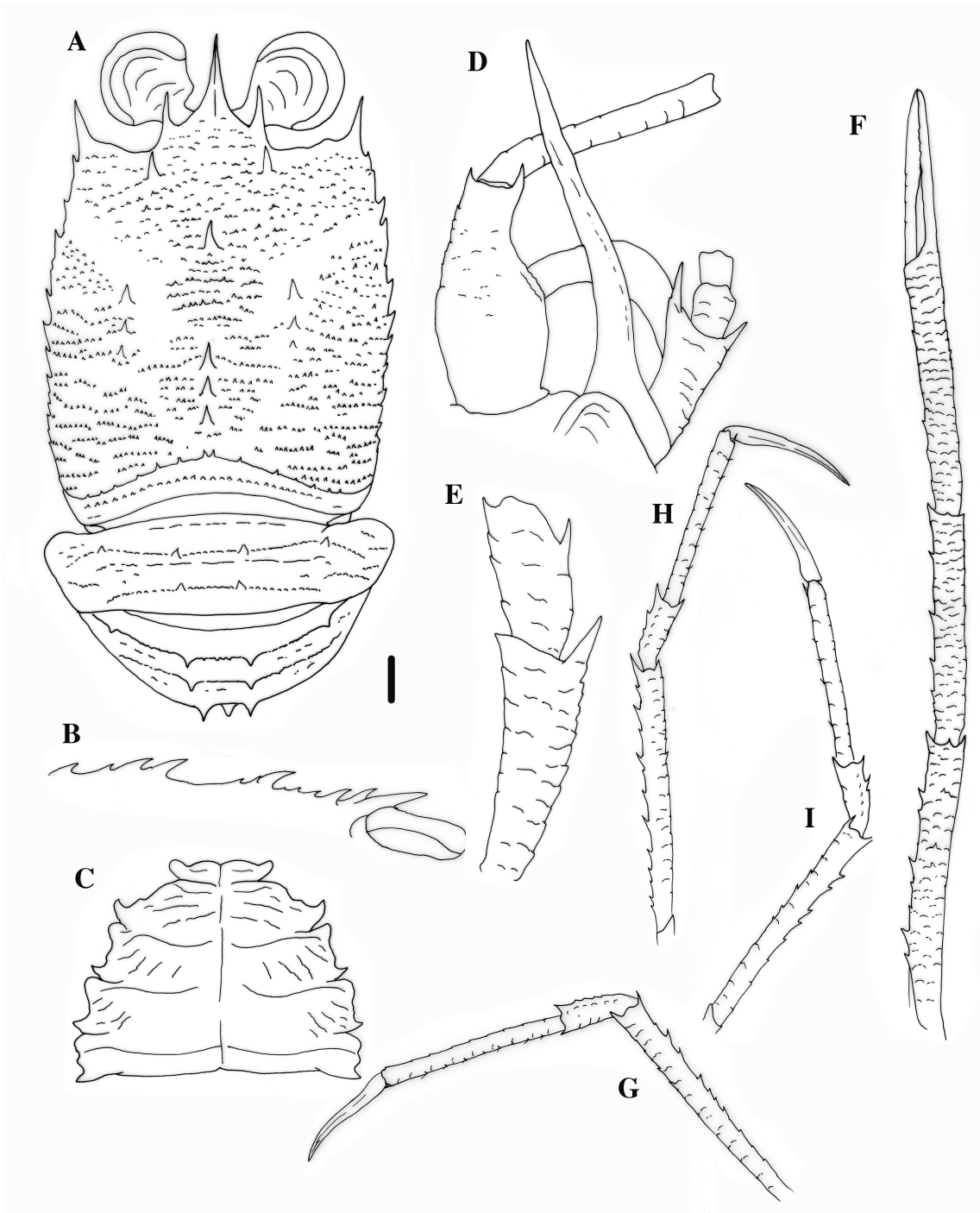


FIGURE 4. *Paramunida crinita* n. sp. male holotype, 7.8 mm (MNHN-Ga xxx). Philippines. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, left P2, lateral view. H, right P3, lateral view. I, left P4, lateral view. Scale: 1 mm.

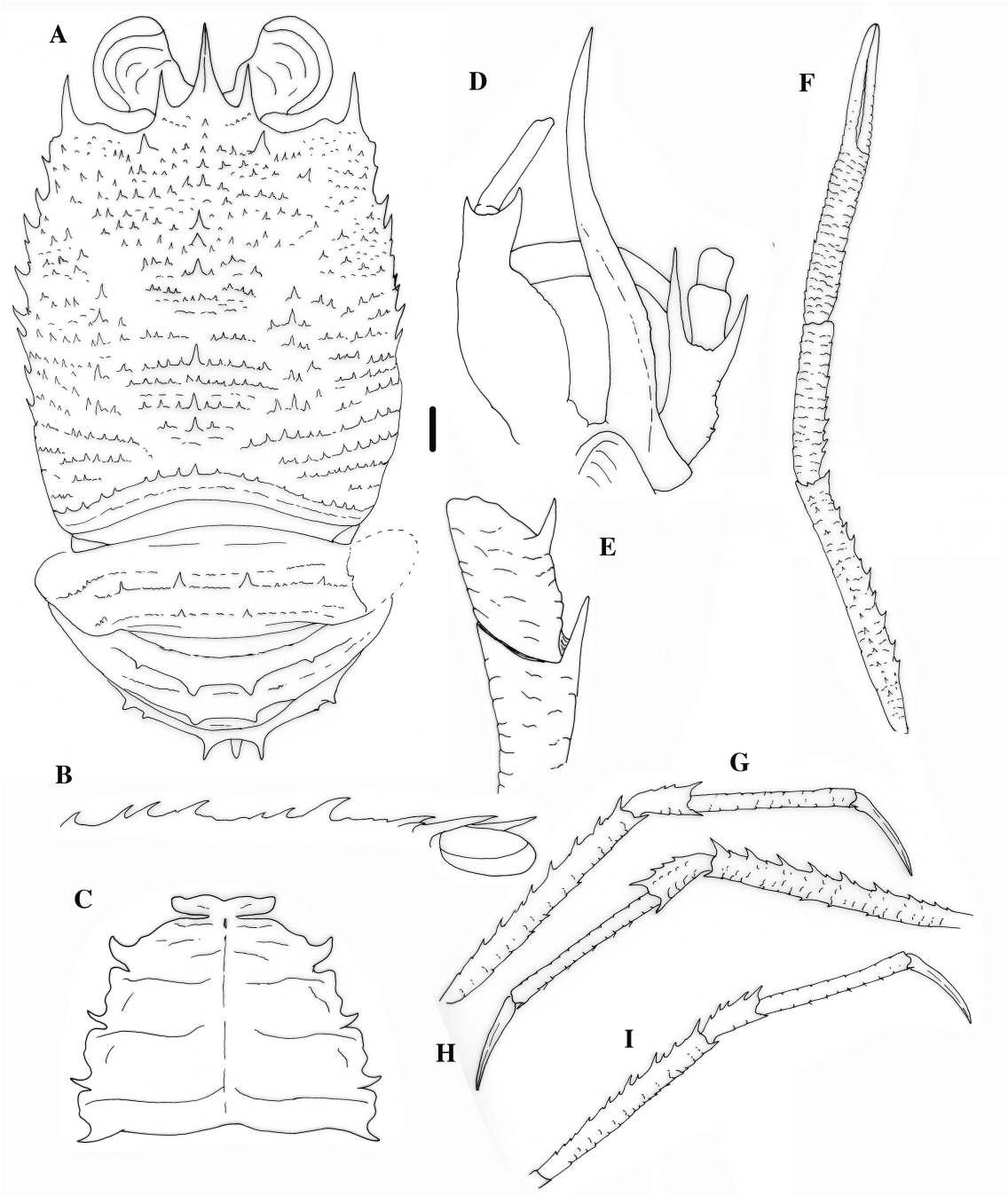


FIGURE 5. *Paramunida marionis* n. sp. male holotype, 10.7 mm (MNHN-Ga xxx). Madagascar. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, left P1, lateral view. G, right P2, lateral view. H, left P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

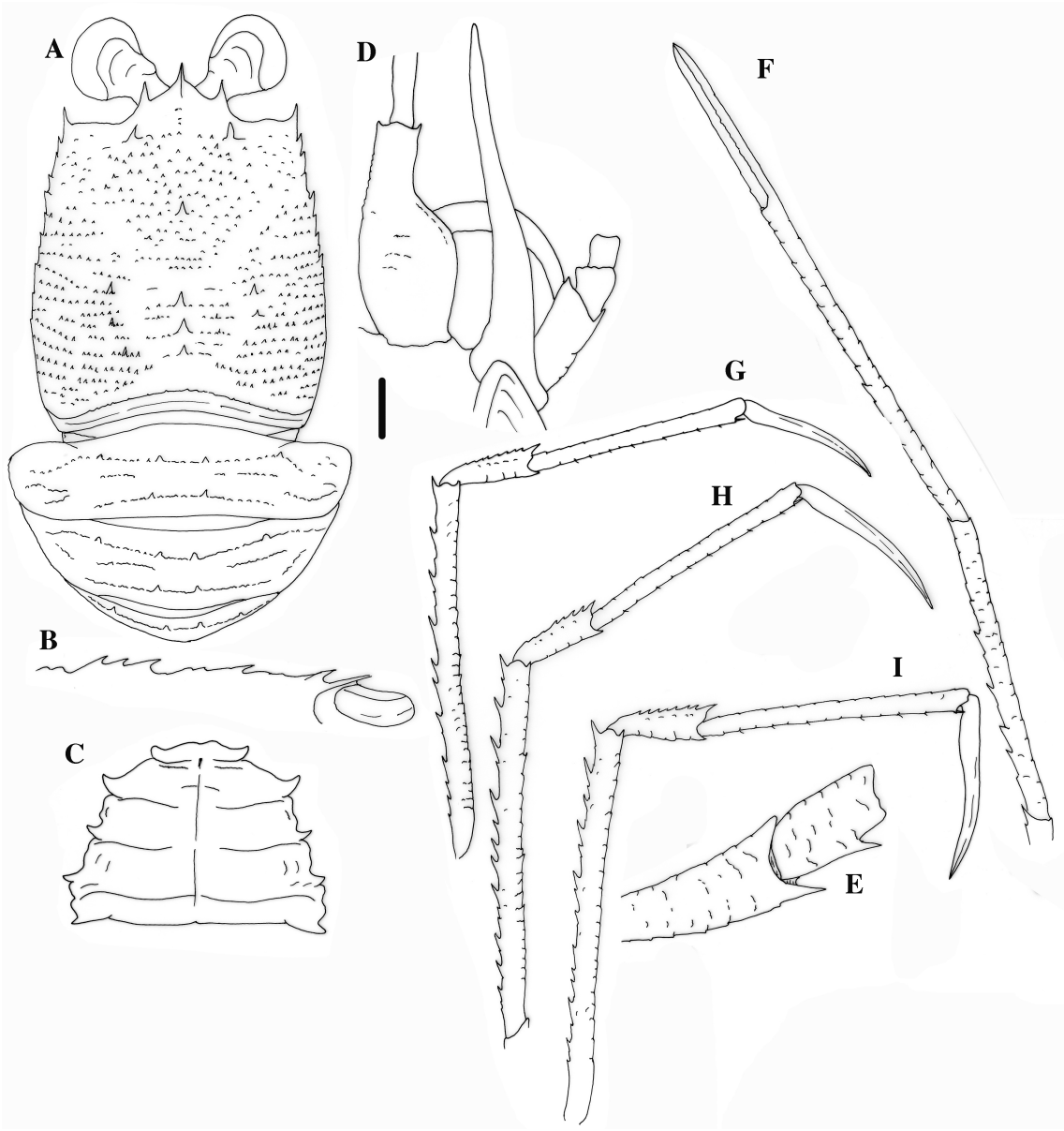


FIGURE 6. *Paramunida microrhina* n. sp. ovigerous female holotype, 5.1 mm (MNHN-Ga xxx). Chesterfield Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, left antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

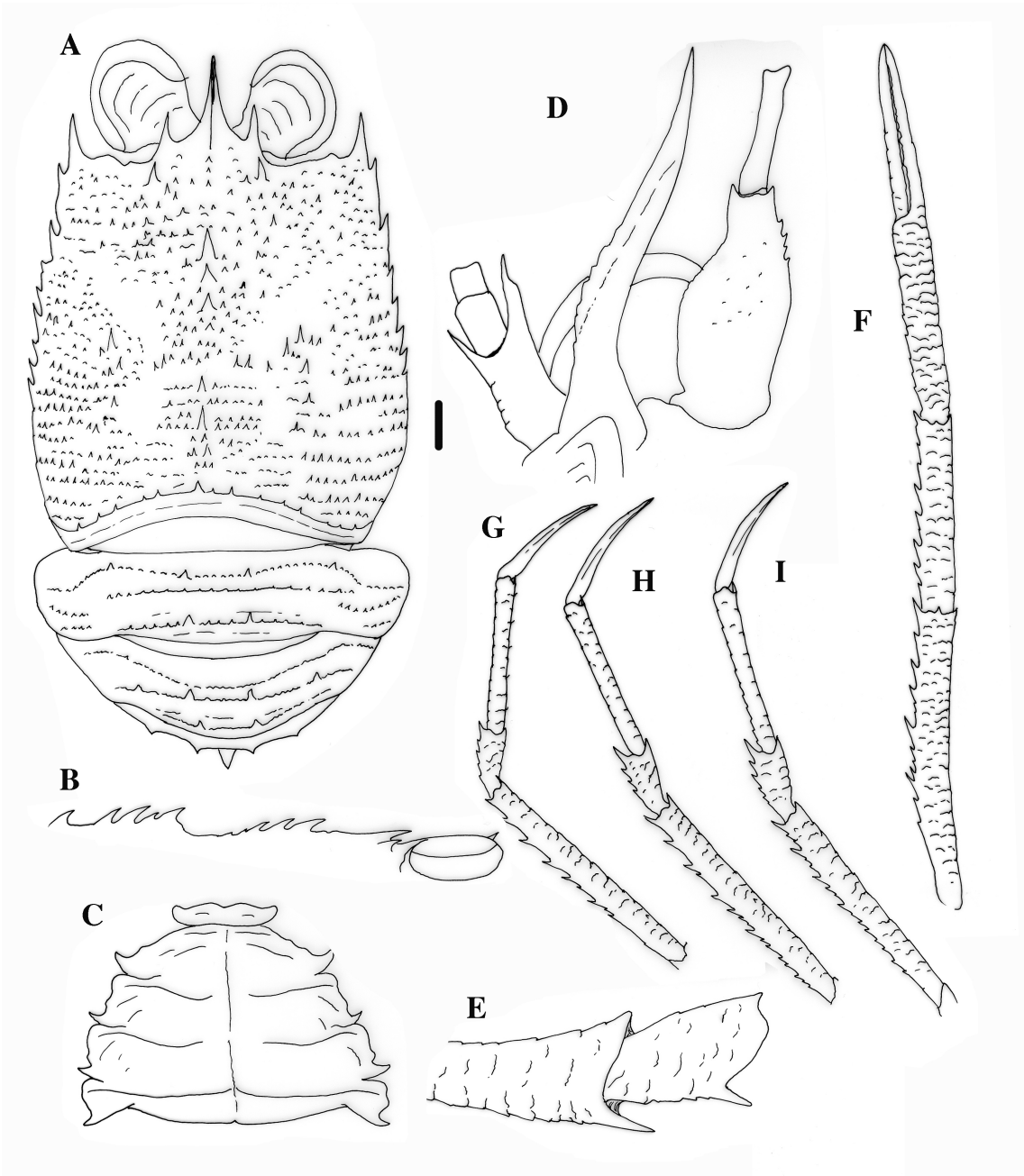


FIGURE 7. *Paramunida mozambica* n. sp. ovigerous female holotype, 6.9 mm (MNHN-Ga xxx). Mozambique. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

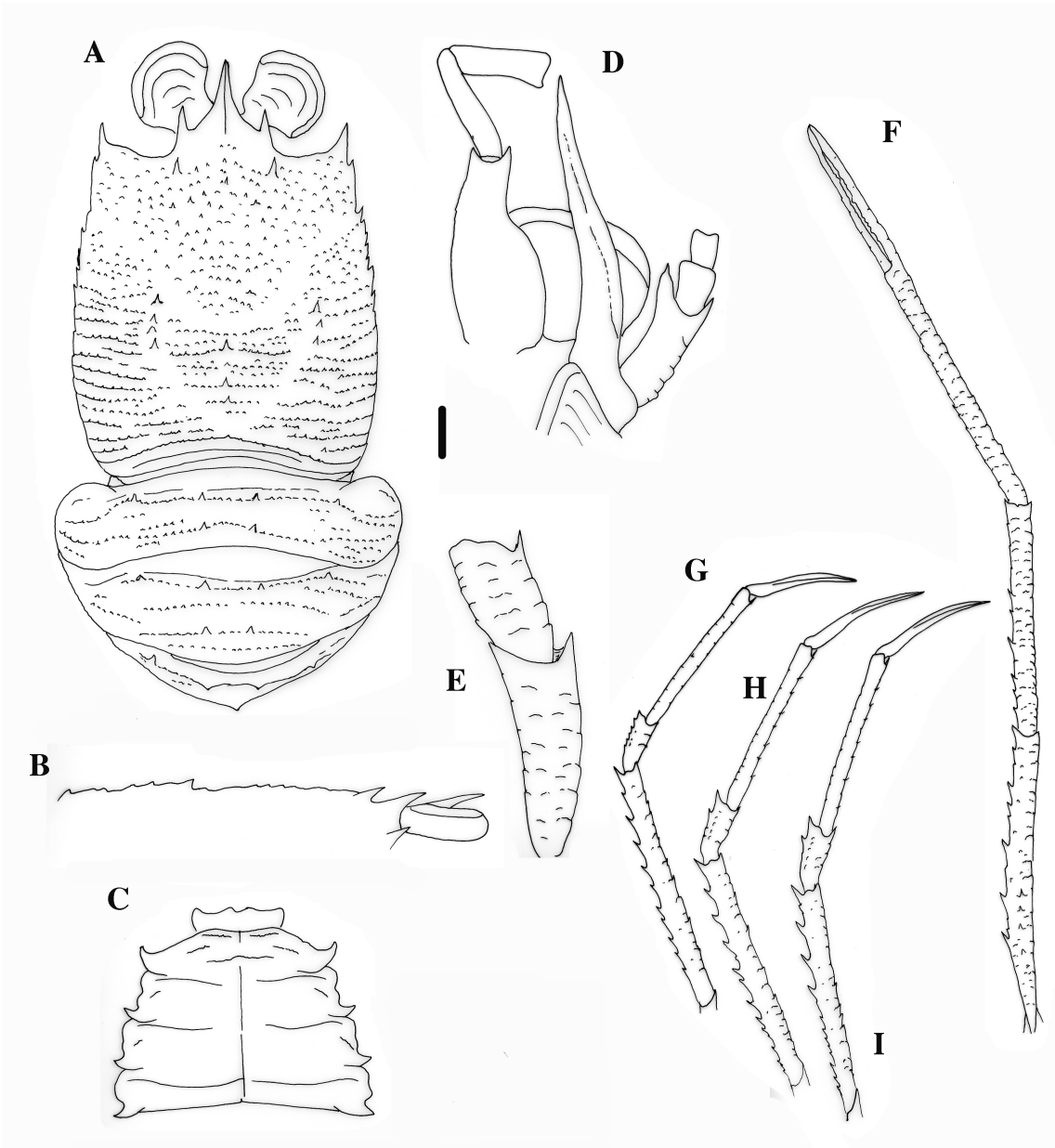


FIGURE 8. *Paramunida parvispina* n. sp. ovigerous female holotype, 7.0 mm (MNHN-Ga xxx). Chesterfield Islands. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

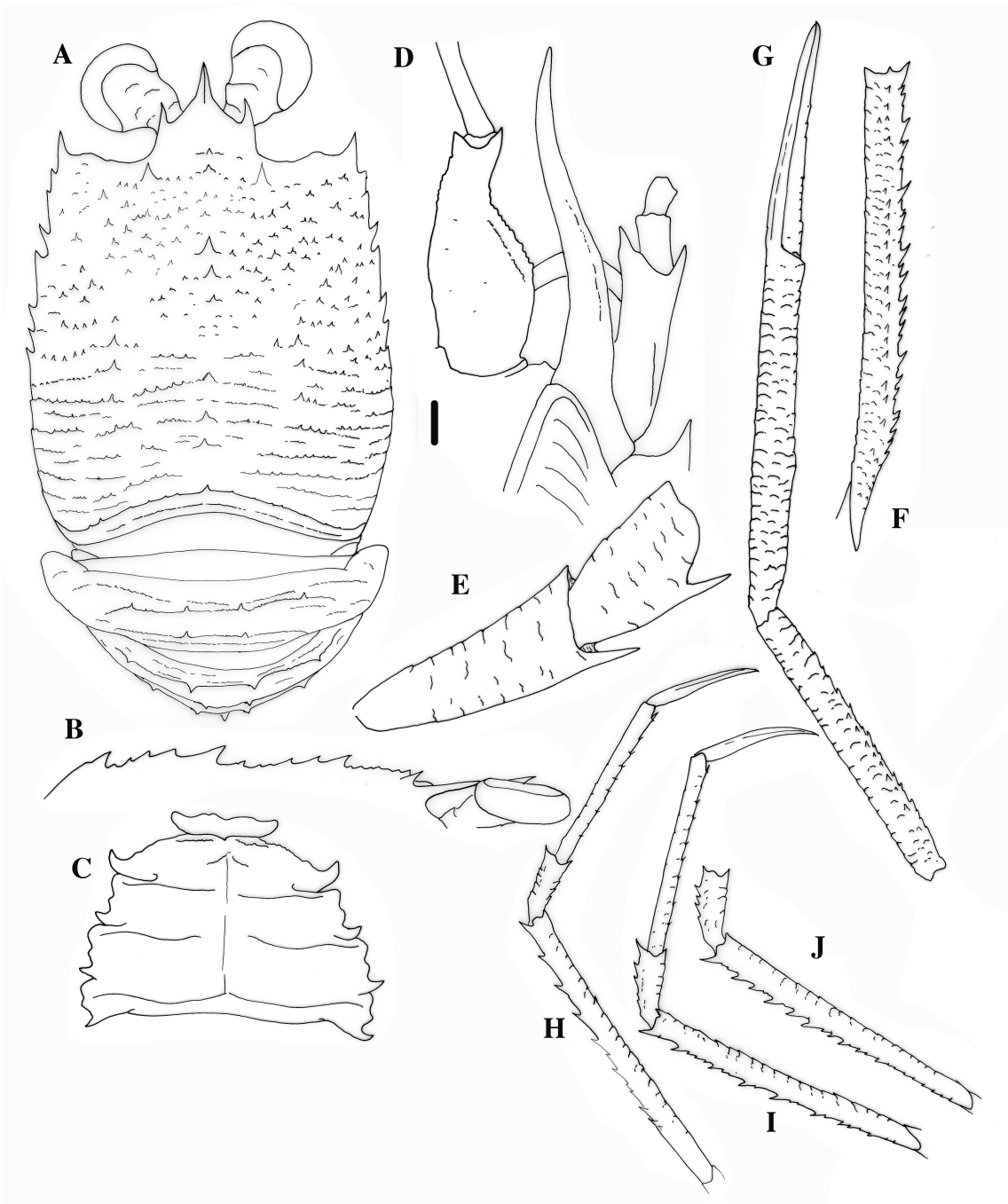


FIGURE 9. *Paramunida poorei* n. sp. male holotype, 9.3 mm (MNHN-Ga xxx). French Polynesia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

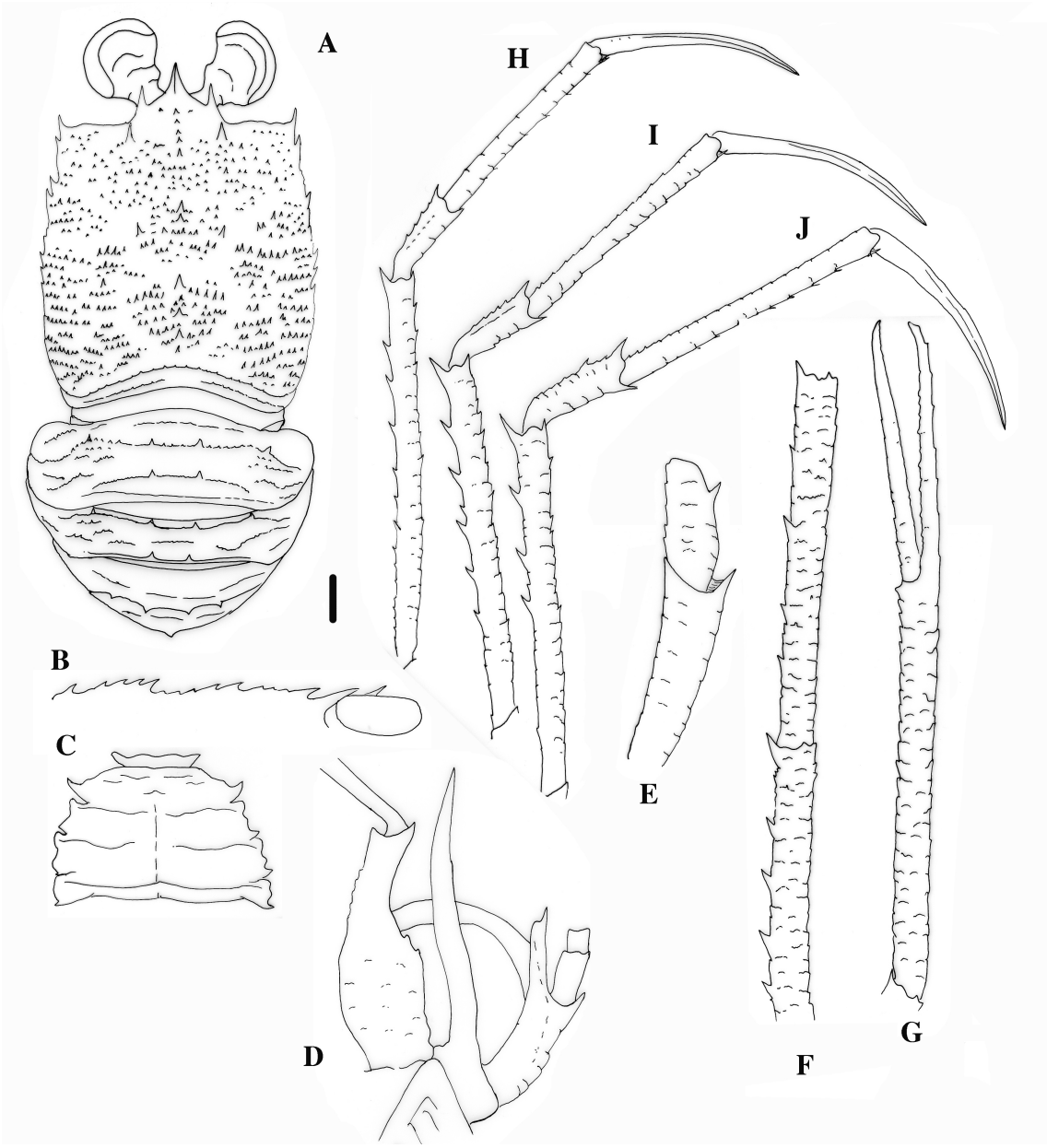


FIGURE 10. *Paramunida spica* n. sp. ovigerous female holotype, 7.1 mm (MNHN-Ga xxx). Vanuatu. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1, lateral view. G, right P2, lateral view. H, right P3, lateral view. I, right P4, lateral view. Scale: 1 mm.

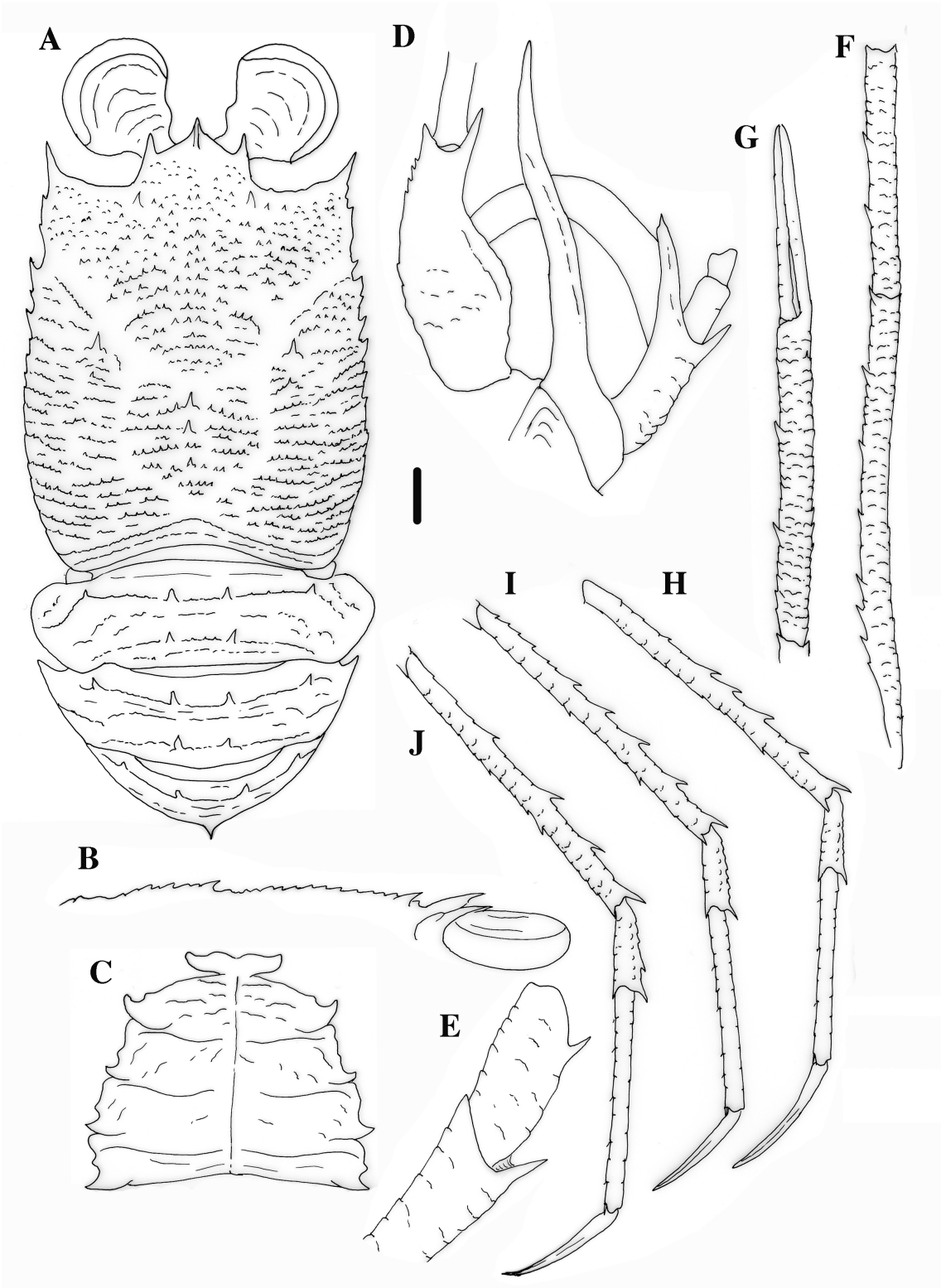


FIGURE 11. *Paramunida tenera* n. sp. male holotype, 8.0 mm (MNHN-Ga xxx). New Caledonia. A, carapace and abdomen, dorsal view. B, carapace, lateral view. C, sternum. D, right antennule and antenna, ventral view. E, right maxilliped 3, lateral view. F, right P1 merus and carpus, lateral view. G, right P1 palm and fingers. H, right P2, lateral view. I, right P3, lateral view. J, right P4, lateral view. Scale: 1 mm.

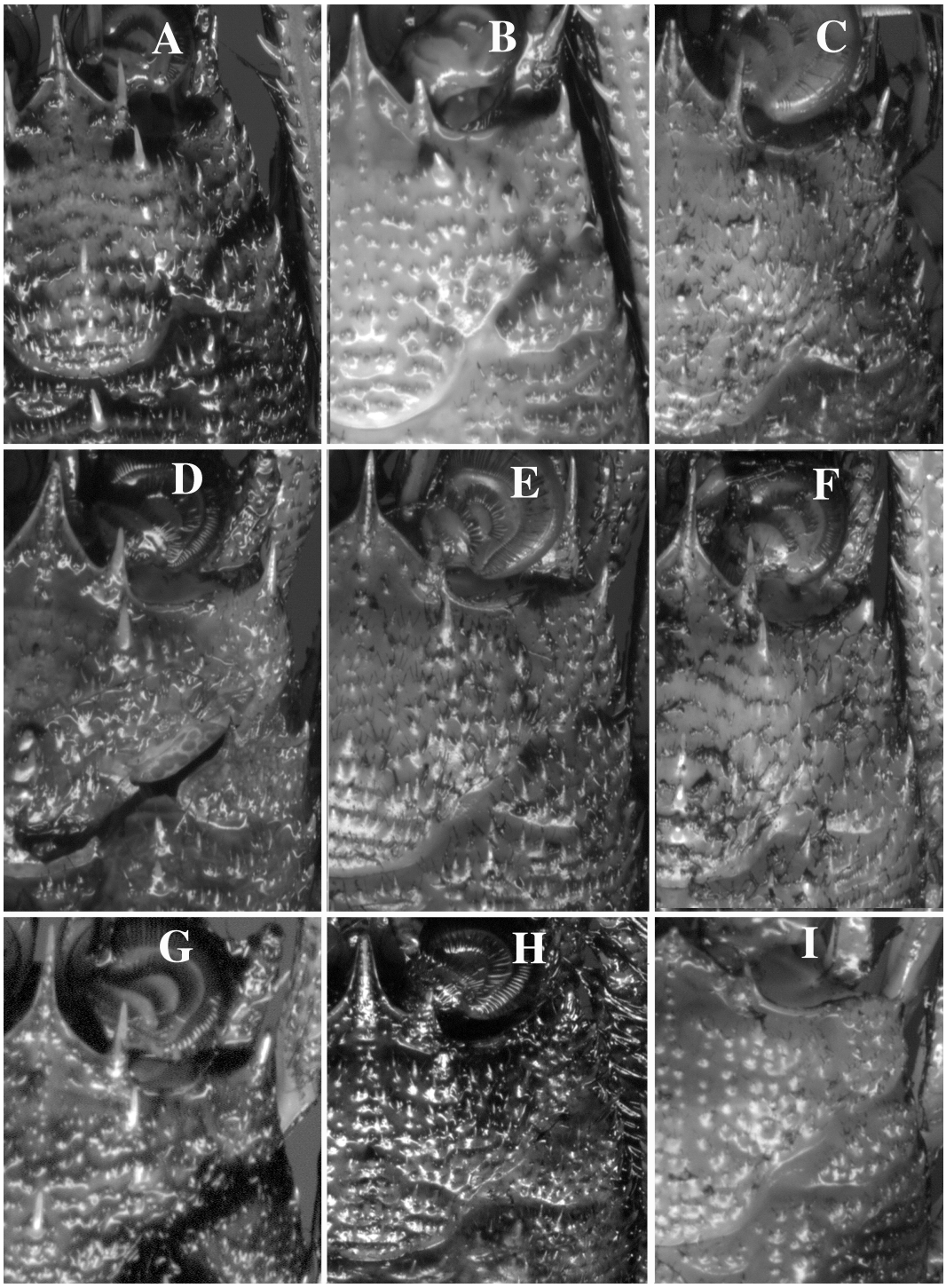


FIGURE 12. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida achernar*, holotype, ovigerous female 9.6 mm. B, *Paramunida amphitrita*, LIFOU, Stn DW15, male 10.3 mm. C, *Paramunida antares*, holotype, male 9.0 mm. D, *Paramunida ascella*, holotype, male 10.9 mm. E, *Paramunida belone*, MUSORSTOM 8, Stn CP963, male 12.0 mm. F, *Paramunida cretata*, BORDAU 1, Stn CP1412, ovigerous female 10.9 mm. G, *Paramunida crinita*, holotype, male 7.8 mm. H, *Paramunida cristata*, Taiwan, Stn CP269, female 10.1 mm. I, *Paramunida curvata*, MUSORSTOM 10, Stn CP1389, ovigerous female 8.8 mm.

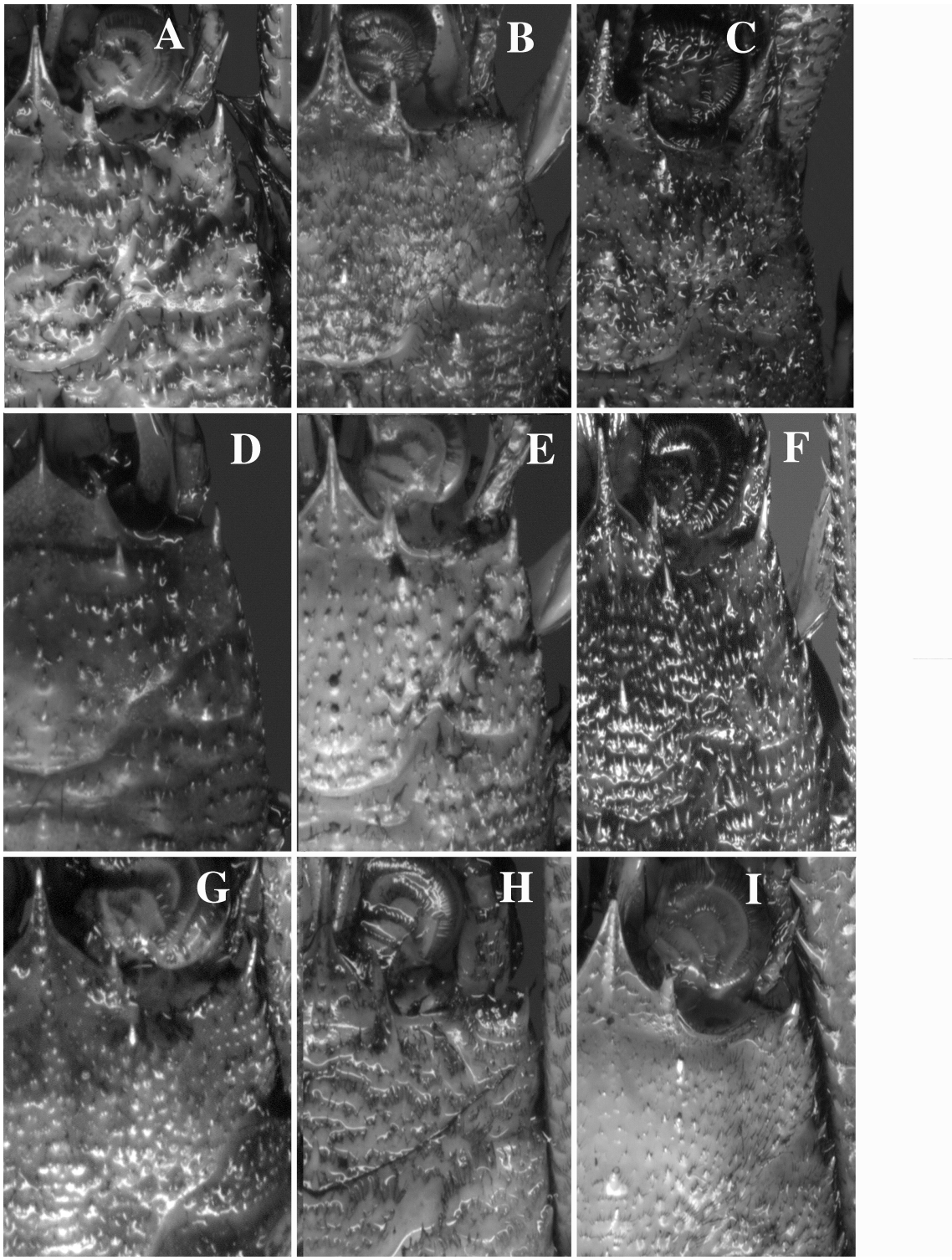


FIGURE 13. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida echinata*, MUSORSTOM 9, Stn CP963, male 12.0 mm. B, *Paramunida evexa*, KARUBAR, Stn CP86, male 9.1 mm. C, *Paramunida granulata*, MUSORSTOM 8, Stn CP971, male 8.3 mm. D, *Paramunida hawaiiensis*, Hawaii, male 9.3 mm. E, *Paramunida labis*, MUSORSTOM 8, Stn CP1027, male 12.0 mm. F, *Paramunida leptotes*, Taiwan, Stn CD380, holotype, male 10.3 mm. G, *Paramunida longior*, BATHUS, Stn CP742, male 9.4 mm. H, *Paramunida lophia*, SALOMON 2, Stn 2199, male 9.7 mm. I, *Paramunida luminata*, MUSORSTOM 7, Stn 629, male 12.6 mm.

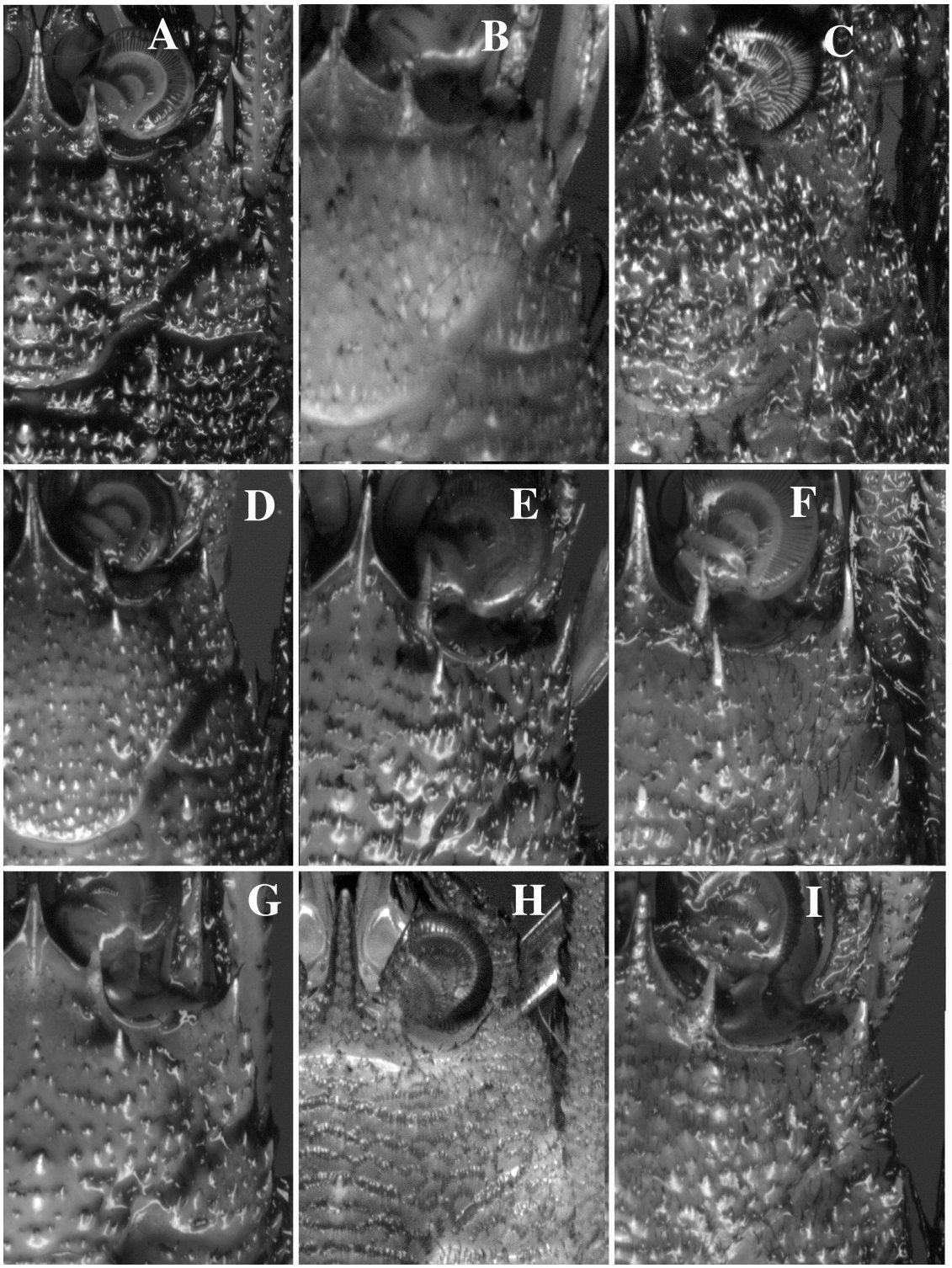


FIGURE 14. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida marionis*, holotype male 10.7 mm. B, *Paramunida microrhina*, holotype ovigerous female 5.1 mm. C, *Paramunida mozambica*, holotype, ovigerous female 6.9 mm. D, *Paramunida parvispina*, holotype, ovigerous female 7.0 mm. E, *Paramunida pictura*, MUSORSTOM 8, Stn CP1025, male 8.7 mm. F, *Paramunida polita*, KARUBAR, Stn CP35, female 12.6 mm. G, *Paramunida poorei*, holotype, male 9.3 mm. H, *Paramunida pronoe*, NORFOLK 1, Stn CP1670, ovigerous female 7.7 mm. I, *Paramunida proxima*, SALOMON 1, Stn CP1831, male 11.8 mm.

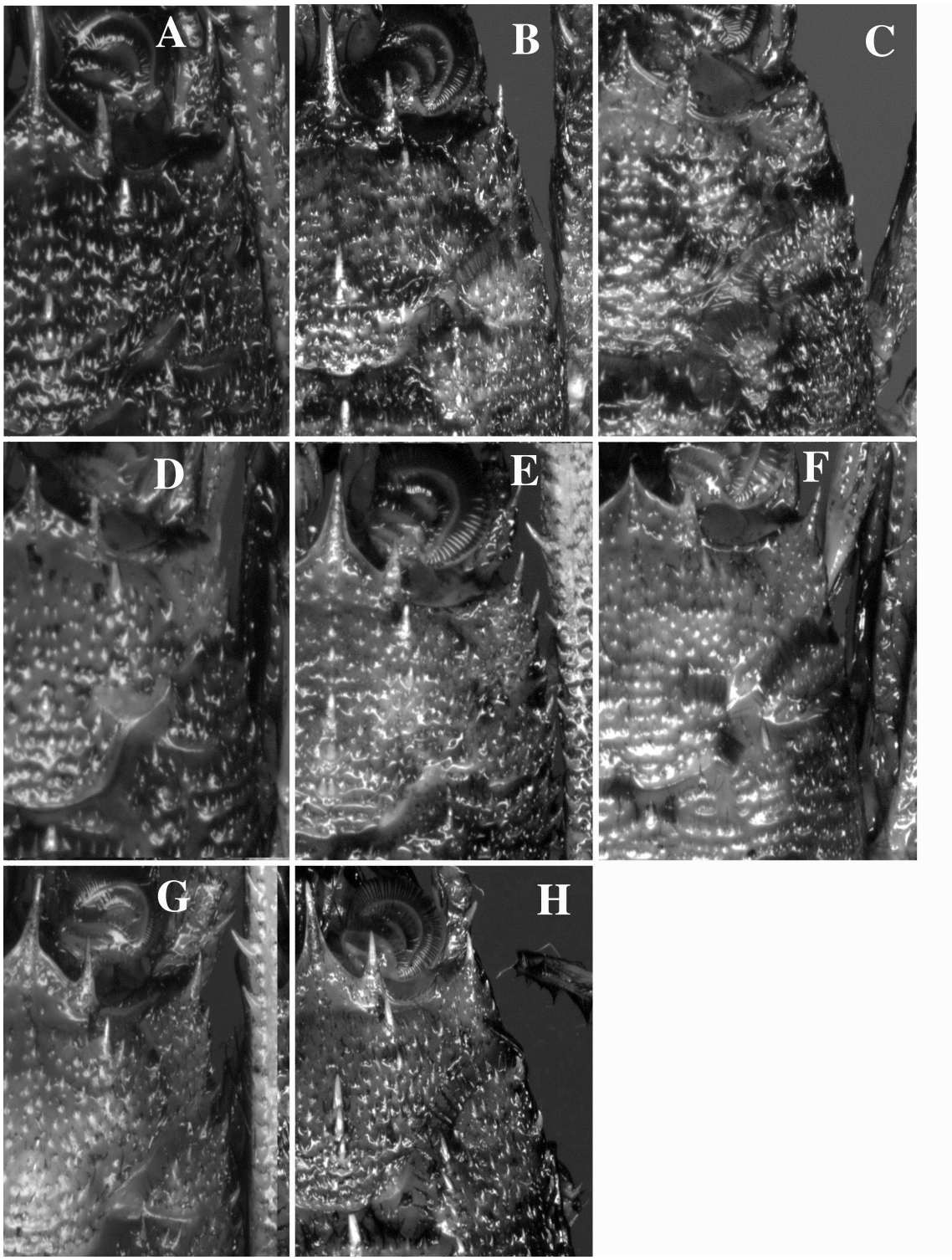


FIGURE 15. Right anterolateral surface of the carapace, dorsal view. A, *Paramunida salai*, SALOMON 1, Stn CP1831, male 10.2 mm. B, *Paramunida scabra*, KARUBAR, Stn CP86, male 11.6 mm. C, *Paramunida setigera*, MUSORSTOM 3, Stn 139, ovigerous female 10.6 mm. D, *Paramunida spica*, holotype, ovigerous female 7.1 mm. E, *Paramunida stichas*, HALIPRO 1, Stn Stn CP877, female 8.9 mm. F, *Paramunida tenera*, holotype, male 8.0 mm. G, *Paramunida thalie*, EBISCO, Stn CP2632, male 8.8 mm. H, *Paramunida tricarinata*, MUSORSTOM 2, Stn CP35, ovigerous female 9.8 mm.

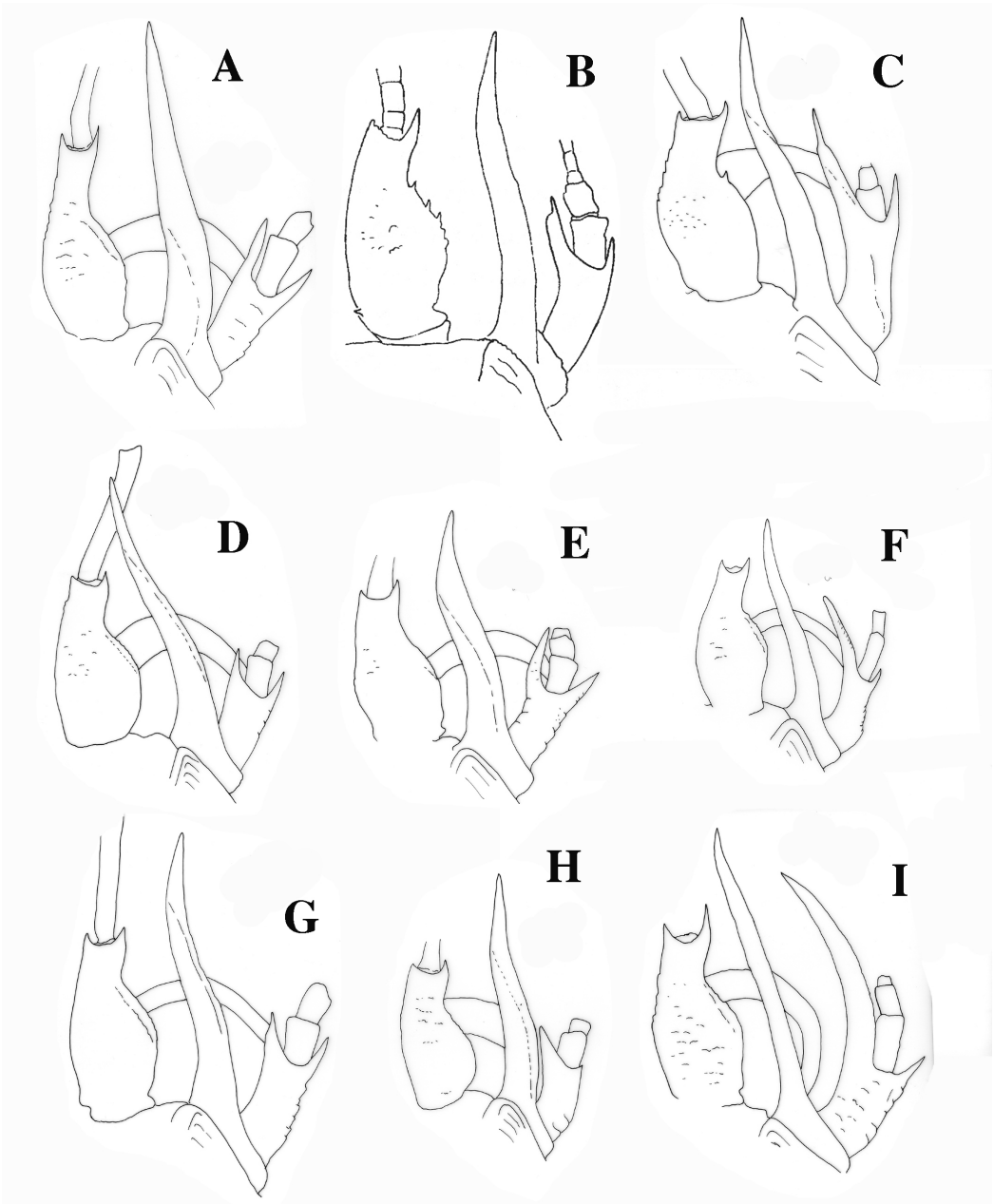


FIGURE 16. Left antennule and antenna, ventral view. A, *Paramunida amphitrita*, LIFOU, Stn DW1650, ov. F 10.5 mm. B, *Paramunida antipodes* (from Ahyong & Poore, 2004). C, *Paramunida belone*, MUSORSTOM 8, Stn 963, male 12.0 mm. D, *Paramunida cretata*, BORDAU 1, Stn CP1412, ovgerous female 10.9 mm. E, *Paramunida cristata*, Taiwan female 10.1 mm. F, *Paramunida curvata*, MUSORSTOM 10, Stn 1390, ovigerous female 10.0 mm. G, *Paramunida echinata*, MUSORSTOM 9, Stn CP1176, male 13.4 mm. H, *Paramunida evexa*, KARUBAR, Stn CP86, male 10.6 mm. I, *Paramunida granulata*, MUSORSTOM 8, Stn CP1027, male 12.4 mm.

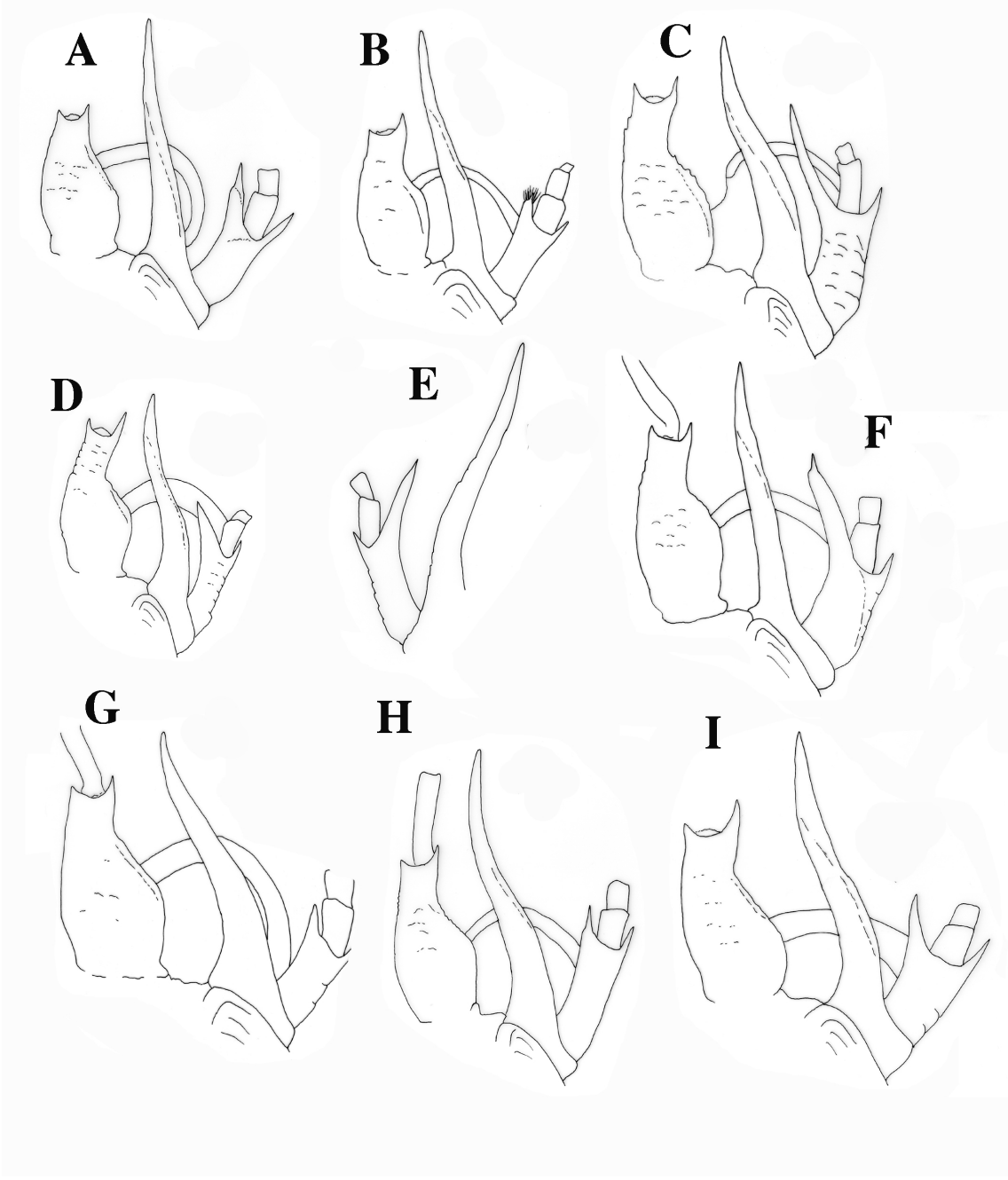


FIGURE. 17. Left antennule and antenna, ventral view. A, *Paramunida hawaiiensis*, Hawaii, M 9.3 mm. B, *Paramunida labis*, MUSORSTOM 8, Stn CP971, female 8.3 mm. C, *Paramunida leptotes*, Taiwan, ovigerous female 12.8 mm. D, *Paramunida longior*, BATHUS 2, Stn CP742, male 9.6 mm. F, *Paramunida lophia*, SALOMON 2, Stn 2199, male 11.8 mm. G, *Paramunida luminata*, MUSORSTOM 7, Stn 629, male 11.4 mm. H, *Paramunida pictura*, MUSORSTOM 8, Stn 1025, male 9.8 mm. I, *Paramunida polita*, KARUBAR, Stn CP86, male 11.6 mm. Right antenna, ventral view. E, *Paramunida longior*, holotype, 8.5 mm.

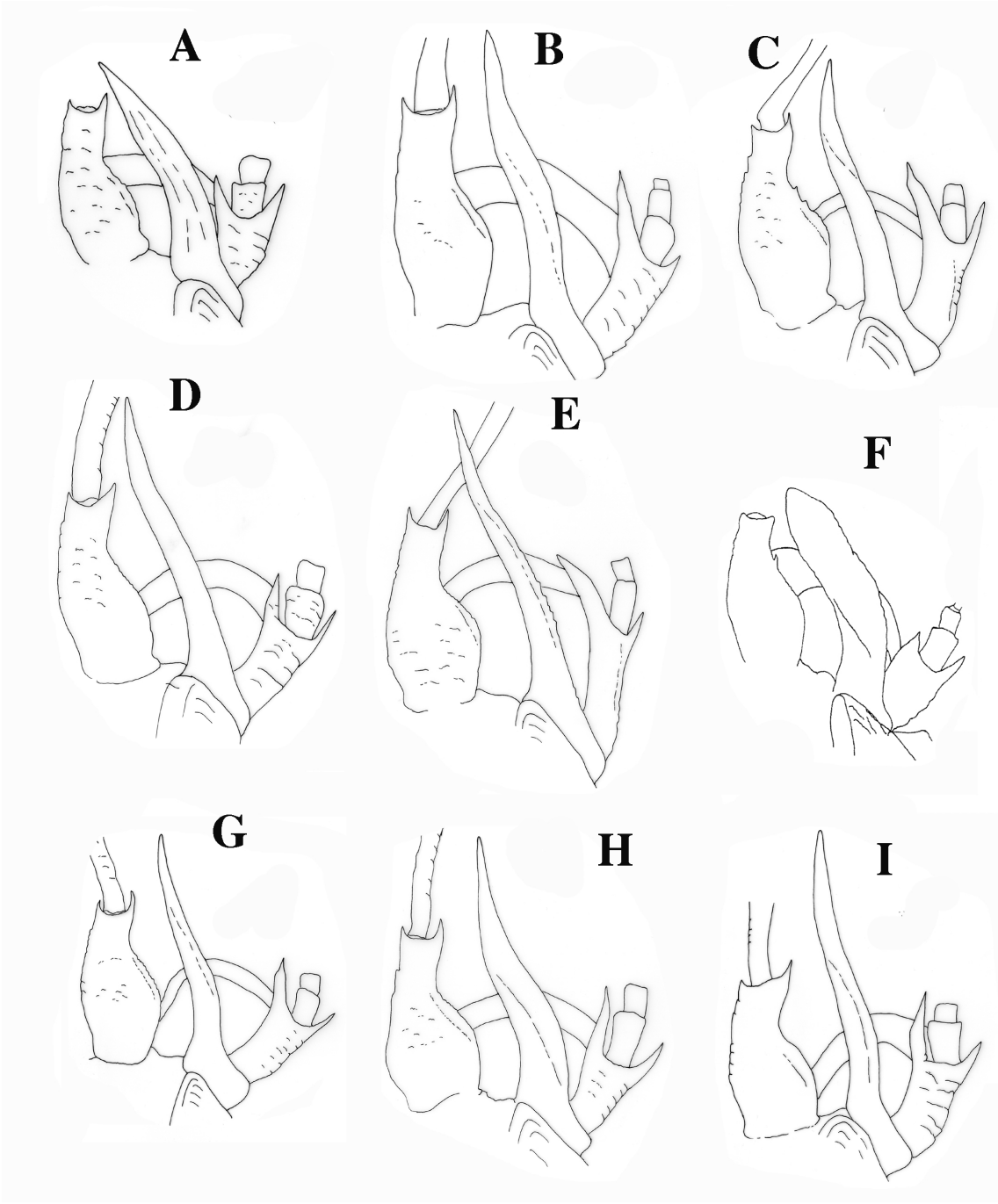
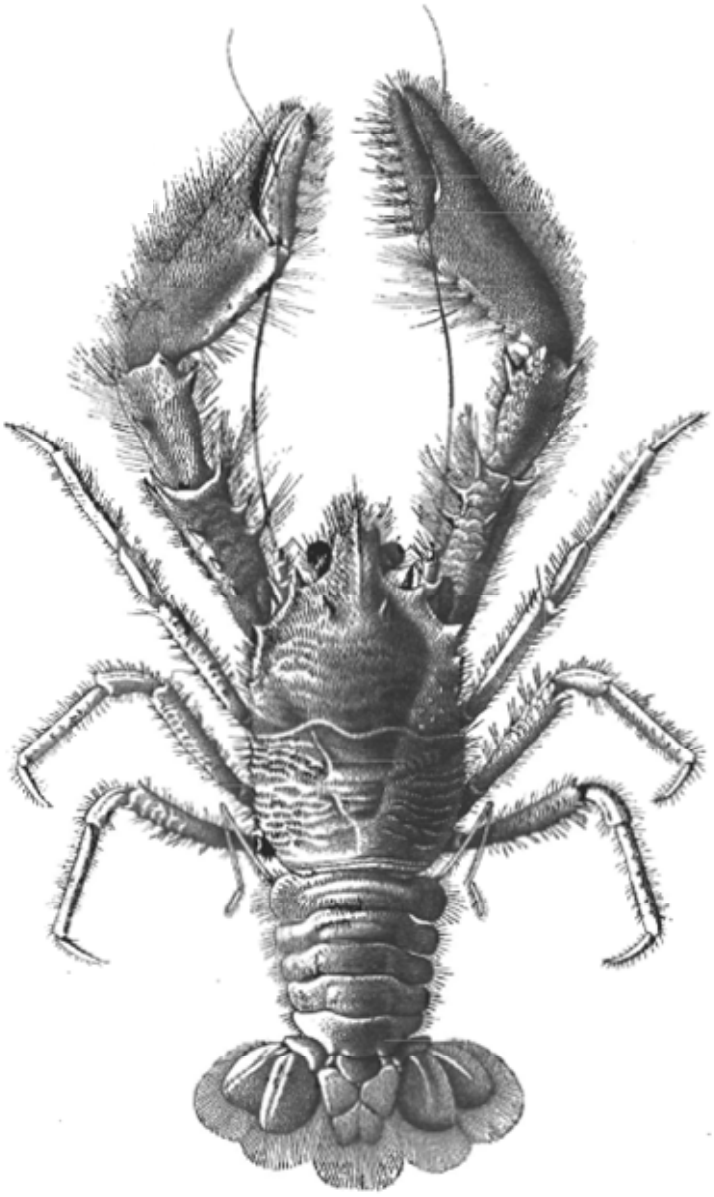


FIGURE. 18. Left antennule and antenna, ventral view. A, *Paramunida pronoe*, NORFOLK 1, Stn CP1670, ovigerous female 8.3 mm. B, *Paramunida proxima*, SALOMON 1, CP1831, male 11.6 mm. C, *Paramunida salai*, SALOMON 1, Stn CP1831, male 11.0 mm. D, *Paramunida scabra*, KARUBAR, Stn 86, male 10.4 mm. E, *Paramunida setigera*, MUSORSTOM 3, Stn 139, male 10.3 mm. F, *Paramunida spatula*, BENTHAUS, Stn DW1897, holotype, male 9.4 mm (from Macpherson, 2006). G, *Paramunida stichas*, HALIPRO 1, Stn CP877, ovigerous female 11.0 mm. H, *Paramunida thalie*, EBISCO, Stn CP2632, male 8.8 mm. I, *Paramunida tricarinata*, MUSORSTOM 2, Stn 35, male 9.0 mm.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1 *O.alaini*	-	16.09	17.17	15.87	17.51	15.14	15.39	18.29	15.87	15.63	16.98	18.70	16.74	16.45	15.22	16.74	15.77	17.30	17.91	18.26	15.43	16.55	16.09	15.87	17.92	15.51	15.43	16.20	16.46	18.35	15.65	15.76	16.58	15.47	16.94	15.56	16.76
2 *P.achernar*	9.79	-	13.48	13.91	12.73	9.69	9.48	11.59	13.26	7.57	9.13	12.28	12.17	9.06	10.65	16.74	6.99	11.19	14.35	12.17	9.35	12.93	10.87	12.34	8.49	9.46	11.30	12.39	10.21	11.96	10.83	14.24	12.77	9.08	12.39	12.35	10.24
3 *P.aff.longior*	10.87	7.43	-	14.78	16.16	14.05	14.92	15.18	17.83	14.65	15.04	16.20	15.65	14.64	15.87	18.91	13.99	15.55	7.39	15.22	15.22	18.40	15.18	16.25	16.61	14.07	16.74	14.89	13.95	14.43	15.87	14.73	17.78	13.04	14.40	16.37	14.15
4 *P.aff.setigera*	11.77	7.82	7.65	-	11.96	13.21	12.49	13.93	15.43	13.57	12.59	15.33	12.61	12.97	13.91	18.48	12.35	15.13	14.39	14.35	14.78	14.39	15.61	13.75	14.88	13.69	13.70	14.35	12.81	14.13	12.36	5.71	15.83	13.35	8.90	15.67	13.50
5 *P.amphitrita*	10.23	4.97	10.06	8.79	-	11.44	12.68	11.97	16.70	13.68	12.06	14.52	11.42	12.62	11.96	19.42	12.08	12.51	15.72	12.57	12.29	13.11	12.03	12.16	12.42	12.31	14.90	13.65	11.56	13.00	11.21	12.51	13.44	10.98	12.74	11.16	13.57
6 *P.antares*	8.76	3.67	6.85	8.18	4.85	-	12.66	12.29	13.86	11.16	11.06	12.64	12.12	10.92	10.99	16.86	9.74	10.53	14.38	12.35	5.49	12.91	12.92	13.39	12.69	9.40	11.43	12.00	10.44	11.86	9.89	13.54	12.22	11.29	12.10	11.40	12.10
7 *P.ascella*	10.52	6.70	7.84	10.14	7.88	6.16	-	12.50	15.19	9.12	2.51	12.16	11.24	8.51	11.25	17.67	7.53	12.82	14.02	13.85	12.66	13.77	11.47	11.86	11.99	9.03	11.96	12.68	10.80	12.41	10.61	12.76	12.81	9.90	12.57	11.22	2.06
8 *P.belone*	8.38	4.28	7.02	8.99	5.90	4.15	6.76	-	15.05	13.74	11.02	13.70	12.20	12.53	12.02	20.66	10.63	11.41	14.47	4.56	13.05	13.56	12.22	12.63	12.76	10.94	13.49	12.78	10.94	3.87	10.57	14.48	10.85	10.48	12.47	13.31	12.32
9 *P.concava*	9.38	11.91	9.97	11.86	12.70	10.37	11.00	11.07	-	15.09	14.99	15.87	17.17	14.93	15.43	15.00	13.17	16.44	19.00	14.78	14.57	16.12	15.47	15.92	15.67	15.84	16.63	16.20	14.33	14.78	14.24	16.14	16.04	13.87	14.33	16.05	16.11
10 *P.cretata*	9.77	2.83	7.96	8.76	5.12	4.75	5.30	4.90	11.49	-	9.45	13.83	13.12	9.57	11.60	17.80	10.18	11.78	14.13	13.46	10.62	14.57	11.24	12.15	11.72	10	13.02	11.39	11.12	13.42	10.70	14.05	14.35	11.48	12.72	12.43	9.43
11 *P.crinita*	10.35	6.25	6.94	8.55	7.87	5.71	1.18	6.53	10.99	5.75	-	13.79	11.34	7.98	10.30	18.90	6.23	11.91	13.86	13.47	12.20	12.43	11.17	12.34	11.35	8.50	11.51	12.18	9.56	12.07	10.23	13.09	12.63	9.04	11.58	12.21	2.19
12 *P.cristata*	10.73	5.55	9.74	9.63	6.24	5.45	7.82	5.15	12.74	5.29	8.46	-	13.48	13.26	12.50	18.80	13.79	13.68	16.02	15.11	13.15	17.00	14.70	14.81	13.54	13.02	15.00	14.67	13.25	14.00	13.33	15.76	15.73	12.33	14.18	14.69	13.96
13 *P.curvata*	11.30	8.16	9.44	10.84	9.22	7.13	7.65	7.30	11.79	7.41	7.90	7.90	-	12.41	10.60	19.08	10.53	11.82	14.39	12.45	12.61	12.58	10.23	13.32	13.50	12.93	14.13	13.26	9.24	12.88	9.22	13.37	15.12	9.71	11.56	12.78	13.20
14 *P.echinata*	9.46	2.90	6.93	8.27	4.72	2.80	4.20	3.39	11.17	3.28	3.76	4.90	6.97	-	11.09	18.12	8.49	12.50	13.23	13.70	10.65	12.60	12.62	12.26	11.61	9.70	11.27	12.17	10.55	13.19	11.78	12.63	12.30	9.76	12.45	12.89	8.49
15 *P.evexa*	10.43	5.13	8.08	9.81	7.42	6.13	8.73	5.40	12.06	5.81	8.49	7.45	8.30	5.81	-	17.17	10.98	10.74	14.22	12.61	10.65	13.59	9.68	12.28	13.50	10.80	14.13	14.13	9.46	13.04	8.26	13.37	13.42	9.33	13.65	12.84	11.54
16 *P.granulata*	12.10	9.45	10.14	11.90	11.16	8.26	10.41	10.10	11.44	9.47	10.59	9.25	10.81	8.60	10.05	-	17.80	17.71	19.57	19.35	17.61	18.56	17.72	18.75	17.48	18.03	17.72	18.48	17.02	19.61	19.06	19.73	20.06	16.41	19.50	18.87	18.50
17 *P.labis*	9.29	5.67	6.98	8.14	6.12	4.66	3.34	5.26	10.96	5.16	2.75	7.13	7.90	3.17	7.46	9.72	-	11.47	13.89	11.63	10.55	11.70	9.91	11.47	10.43	9.47	11.09	10.68	9.38	11.15	9.46	11.95	13.18	8.72	11.63	11.72	8.25
18 *P.leptotes*	9.72	4.75	7.20	9.01	7.40	4.84	6.25	4.77	10.22	4.26	5.39	6.84	7.86	4.25	6.50	9.25	5.65	-	15.60	13.18	10.74	14.91	10.56	12.94	11.62	12.81	12.72	11.84	11.06	13.74	11.16	15.51	14.79	10.82	14.27	13.15	12.28
19 *P.longior*	10.42	7.42	1.99	7.84	9.65	6.86	8.08	7.24	9.75	8.13	7.39	9.18	9.69	7.38	8.97	9.28	7.42	7.44	-	14.30	15.00	16.85	15.66	15.43	16.22	13.18	15.26	15.65	12.62	14.34	16.52	13.90	16.74	12.82	12.38	16.66	13.59
20 *P.lophia*	9.11	4.41	7.56	9.83	6.01	4.29	6.22	1.71	11.79	5.26	6.40	5.74	7.35	3.71	4.85	10.23	5.06	5.35	8.22	-	12.83	14.78	12.49	13.21	13.86	11.47	14.35	13.48	12.80	3.13	11.23	14.89	13.21	11.81	12.68	14.09	14.60
21 *P.luminata*	10.22	4.89	7.62	8.76	6.07	1.90	7.38	5.34	10.70	5.96	6.47	5.76	7.21	3.56	6.90	8.36	5.64	5.61	7.63	5.50	-	14.07	11.78	12.66	12.63	9.93	11.74	10.87	11.16	13.91	10.18	14.67	13.87	11.94	12.91	11.81	13.07
22 *P.microrhina*	11.93	10.25	12.07	12.68	11.10	10.15	10.41	9.85	13.47	9.97	10.85	10.86	11.38	10.43	11.63	13.25	9.39	12.46	11.89	10.39	11.40	-	15.86	15.13	14.12	12.88	15.00	15.62	12.44	14.74	12.49	14.90	14.86	12.39	12.83	15.65	14.52
23 *P.mozambica*	11.30	6.98	9.25	9.93	8.11	7.11	7.90	7.99	12.48	6.77	8.57	7.42	8.62	6.53	7.81	10.19	6.81	8.78	9.28	7.43	8.13	10.37	-	12.08	13.39	11.59	15.61	13.91	10.92	13.00	9.05	14.38	14.87	10.21	13.88	11.67	12.11
24 *P.parvispina*	11.18	8.28	8.93	10.10	8.72	8.62	11.01	8.35	11.78	9.15	9.72	9.83	10.25	8.61	8.14	12.58	8.65	9.60	9.14	8.94	9.00	12.11	8.46	-	13.01	11.29	14.18	12.72	11.68	13.10	10.82	13.64	14.14	12.05	13.81	11.62	12.91
25 *P.pictura*	9.95	4.12	7.93	8.56	5.97	3.15	5.29	4.06	12.20	4.09	4.84	6.21	8.88	2.59	6.18	10.44	4.16	4.64	8.52	4.41	4.51	10.31	7.12	9.22	-	11.35	9.76	14.22	12.06	13.49	12.23	15.73	15.03	11.04	14.95	12.87	12.86
26 *P.polita*	9.08	4.91	6.98	8.58	6.30	3.68	4.48	3.59	9.91	4.20	4.08	5.99	6.80	3.14	6.27	10.20	4.13	3.84	7.42	3.75	4.68	9.35	7.34	8.96	3.66	-	11.83	11.00	10.02	10.22	11.45	12.73	12.64	10.41	11.86	12.70	9.27
27 *P.poorei*	10.89	4.43	7.38	9.61	6.49	3.00	6.25	4.73	11.82	5.05	5.58	6.43	8.13	3.12	7.15	9.86	4.98	5.16	7.83	5.09	4.22	8.90	7.40	9.58	2.72	4.00	-	14.24	12.35	14.13	13.44	14.84	14.84	13.05	13.48	13.22	11.54
28 *P.pronoe*	11.26	6.95	9.92	11.43	9.19	7.07	8.06	7.02	13.94	5.81	8.51	8.05	9.40	6.45	8.95	11.05	8.04	5.15	10.43	7.54	7.38	11.78	10.26	9.92	7.06	6.52	7.81	-	11.83	13.13	11.52	14.67	15.72	11.65	14.63	13.38	13.28
29 *P.proxima*	8.60	6.05	7.02	8.31	6.78	3.93	7.17	5.53	12.07	6.43	6.73	7.57	8.41	5.09	8.25	10.51	5.18	5.27	7.48	6.16	5.17	10.61	8.19	9.34	5.37	5.56	5.82	7.57	-	11.87	8.33	14.19	13.91	6.47	11.63	11.75	10.44
30 *P.salai*	8.36	4.44	7.37	8.97	5.60	3.43	6.89	1.30	11.41	5.29	6.65	5.10	6.95	3.97	5.34	9.37	5.39	5.36	7.37	1.54	4.64	9.54	7.93	8.93	4.36	3.32	4.67	8.01	5.30	-	11.01	14.46	12.47	11.56	12.51	12.98	13.20
31 *P.scabra*	10.12	4.81	7.51	8.38	5.72	4.47	7.96	4.42	11.18	5.26	7.72	4.45	6.66	4.59	3.21	8.47	6.03	6.18	7.05	4.54	5.26	9.51	5.49	6.96	5.18	4.82	5.46	8.62	6.82	4.13	-	13.55	12.96	9.89	13.52	10.63	11.76
32 *P.setigera*	10.10	6.67	6.37	2.60	8.02	7.08	8.84	7.95	11.24	7.16	7.28	9.04	9.57	7.01	8.31	11.49	6.65	7.53	6.57	8.33	7.72	11.52	8.12	9.38	7.40	6.83	8.12	10.30	7.09	7.47	6.88	-	16.16	13.81	9.15	15.34	13.78
33 *P.spica*	10.00	6.43	8.53	10.54	7.44	5.45	8.25	4.26	11.61	6.19	8.27	5.78	7.26	5.13	6.50	10.96	7.04	6.31	8.76	4.41	6.45	11.15	7.23	8.72	5.57	5.33	6.43	8.08	7.48	4.45	5.49	9.06	-	13.43	16.34	14.47	13.21
34 *P.stichas*	9.30	5.38	7.25	8.77	5.48	3.76	7.20	5.18	12.02	5.56	6.61	6.46	8.40	3.87	7.02	9.07	4.93	5.40	7.09	5.52	4.54	10.11	7.52	8.71	5.12	5.35	5.11	7.25	2.87	4.65	5.42	7.13	6.79	-	11.40	12.44	10.13
35 *P.tenera*	10.97	8.07	6.66	4.71	10.19	7.61	9.08	8.25	11.83	8.91	7.72	9.31	9.58	7.92	8.75	10.37	7.75	9.38	6.19	8.23	8.24	11.30	9.24	10.37	9.07	8.19	8.86	12.00	7.96	7.83	7.08	4.85	10.60	7.86	-	14.72	12.50
36 *P.thalie*	8.84	5.37	8.50	8.05	4.70	4.58	6.00	5.63	12.27	5.10	5.83	6.46	8.30	4.47	6.91	10.27	4.56	7.12	8.08	5.76	5.82	9.54	6.69	9.18	5.07	4.71	6.01	8.90	5.65	5.34	5.22	5.28	6.95	5.76	8.87	-	12.43
37 *P.tricarinata*	11.08	7.36	6.95	9.67	8.78	6.81	1.41	7.42	10.99	6.52	1.13	9.36	8.76	4.88	9.15	10.59	3.77	6.27	7.40	6.84	7.57	11.11	9.26	10.59	5.95	5.17	5.81	9.14	7.84	7.54	8.39	8.41	9.38	7.67	7.96	6.94	-

TABLE 1. Divergences (uncorrected “p” distances, per unit) among specimens analyzed: ND1 (above diagonal) and 16S rRNA (below diagonal).



Munidopsis crinita Faxon, 1893

CAPÍTULO V

Deep under the sea: Unraveling the evolutionary history of the deep-sea squat lobster *Paramunida* (Decapoda, Galatheidae)

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ABSTRACT

The diversification of Indo-Pacific marine faunas has long captivated the attention of evolutionary biologists. Previous studies have mainly focused on coral reef or shallow water associated taxa. Our study represents the first attempt to reconstruct the evolutionary history – systematics, diversification and biogeography – of a deep-sea lineage. We sequenced the molecular markers 16S rRNA, COI, ND1, 18S rRNA and 28S rRNA for more than the 80% of the nominal species of the *Paramunida* genus, including ten undescribed taxa. Analyses of the molecular phylogeny revealed an increase in the rate of diversification in the Oligocene-Miocene boundary followed by a slowdown in the rate of lineage accumulation over the time. The parametric biogeographical reconstruction denoted the importance of the SW Pacific area, specifically the island arc of Fiji, Samoa, Tonga, Vanuatu, Wallis and Futuna, as a center of diversification in galatheids, probably in relation with the high tectonic activity, abrupt palaeoceonagraphic changes and the onset of overall warming occurred during the Oligocene-Miocene period. These results add strong evidence for the existence of a common period of diversification in both shallow and deep-sea waters.

Keywords

Phylogenetics, diversification, divergence times, biogeography, DEC model, deep-sea squat lobster.

INTRODUCTION

Within western Pacific, the Indo-Malayan triangle harbours the highest marine species diversity in the world, which declines westward across the Pacific and eastward across the Indian Ocean (Paulay, 1997; Bellwood & Hughes, 2001). Much work has been conducted in the area in order to ascertain the origin and causes of such diversity, but mainly focused on shallow water or reef associated species (Benzie & Williams, 1997; Alfaro *et al.*, 2007; Williams & Duda, 2008; Malaquías & Reid, 2009). These studies suggest that multiple factors such as sea-level changes, tectonic activity and alterations in ocean currents and temperature regimes are likely to be involved in the shaping of the distribution and diversification of these faunas (Barber & Bellwood, 2005; Williams, 2007; Williams & Duda, 2008). In contrast, there is a limiting number of studies attempting to understand the diversification of marine taxa associated with deep-sea waters, such as those from the continental slope and abyssal plain (200-2000 m), in which the effect of factors such as changes in sea level and temperatures is not as evident as in shallow-water habitats. Yet, a recent study (Macpherson *et al.*, 2010) suggest that both shallow and deep-water faunas are likely to have been driven by similar evolutionary and ecological processes.

Examining the evolutionary and biogeographic history of deep-sea organisms has traditionally been limited by the difficulties to collect samples at such depths. Although taxon sampling is far from being as exhaustive as those from shallow water faunas, after decades of deep-sea surveys, a reasonable taxon sampling is now available for some groups of marine organisms, such as deep-sea squat lobsters (family Galatheidae), to attempt reconstructing their evolutionary history.

Squat lobsters of the family Galatheidae are a very abundant and highly diversified fauna across all marine habitats, although around 80% of the described species are found in the Pacific (Baba, 2005). Although the group has been the focus of increased taxonomic attention, very little is known on its origin and evolutionary diversification (Baba *et al.*, 2008). Previous studies have suggested that the group probably evolved through a rapid, explosive radiation followed by an stasis in morphological diversification (Machordom & Macpherson, 2004). For example, diversification in the genus *Munida* was approximately dated between 7-14 Mya (Middle-Late Miocene), based on average mitochondrial divergence rates from other organisms (Machordom & Macpherson, 2004).

Events of rapid diversification as those proposed for galatheids can be explored using molecular phylogenies to model birth-death rates without needing the fossil record (Crisp & Cook, 2009). These molecular reconstructions can be transformed in lineages-through-time-plot (LTT), which in combination to the diversification estimates can be useful for interpreting the tempo and mode of evolution of a specific group (Rüber *et al.*, 2003; Ribera *et al.*, 2008; Williams & Duda, 2008). In addition, phylogenetic reconstructions have long been used to infer biogeographical history from the distribution patterns of extant species. Classic cladistic biogeographic methods are based on the principle of parsimony, which limits the type of data that can be used in the reconstruction to the tree topology and extant distributions. These methods consider dispersal as a rare, random event that could not give rise to congruent distribution patterns across organisms (Humphries & Parenti, 1999; Sanmartín, 2010). Dispersal was only invoked a posteriori to explain distribution patterns that did not fit the vicariant model (Brooks & McLennan, 2001).

Probably, there is no better scenario for a dispersal-based biogeography than the marine realm, where dispersal is typically considered as the most important process generating biological diversity (Cowie & Holland, 2006). Newly developed parametric methods of biogeographic inference such as maximum likelihood Dispersal-Extinction-Cladogenesis model Lagrange, (Ree *et al.*, 2005; Ree & Smith, 2008) and the Bayesian Island Biogeography method (Sanmartín *et al.*, 2008) allow for the first time to estimate dispersal rates from distribution and phylogenetic data and probabilities of ancestral areas in a given phylogeny (Ree & Smith, 2008). These methods offer the advantage that they allow incorporating temporal information – lineage divergence times and area connectivity through time – to biogeographic inference, thus increasing the accuracy and realism of biogeographic reconstructions (Ree & Sanmartín, 2009; Sanmartín, 2010).

Here, we use the squat lobsters of the genus *Paramunida* as a model to examine the diversification of marine taxa associated with moderately deep waters. Bathymetrically, the genus is typically recorded in transitional depths (200-500 m), with few species occurring in the continental shelf and the upper bathyal depths (Baba, 2005). The genus comprises 26 species distributed across the Indo West Pacific (Baba *et al.*, 2008; Cabezas *et al.*, 2009; Macpherson & Baba, 2009). Most lineages are distributed in the western part, with one lineage extending its range to the Indian Ocean and three species endemic to the Central Pacific Ocean. In terms of distribution, most

species present narrow ranges, restricted to single islands or archipelagos, with some species more widely distributed (see Baba *et al.*, 2008). There is very little data on the biology or ecology of the group, while knowledge on larval development is limited to a few closely related genera such as *Agononida* or *Munida* (Guerao *et al.*, 2006), mainly due to the difficulty in obtaining ovigerous females from the deep-sea.
Morphologically, all species are very similar, showing very subtle differences mainly associated with the spinulation of the carapace, the shape and length of antennal and antennule segments and length of walking legs (Cabezas *et al.*, 2009).
In this paper, we present the first phylogeny of the genus, including 23 of the 26 recognized taxonomic species plus nine additional new species revealed by sequence data and supported by morphological differences. Molecular phylogenies were reconstructed based on mitochondrial (COI, ND1 and 16S rRNA) and nuclear markers (18S rRNA and 28S rRNA) in order to explore: i) phylogenetic relationships among species of *Paramunida*; ii) the timing and tempo of species diversification; iii) the biogeographic history (spatio-temporal evolution) of the group using a parametric approach to ancestral area reconstruction.

MATERIAL AND METHODS

Taxon sampling and identification

Samples were obtained from specimens deposited in the collections of the Muséum National d´ Histoire Naturelle (MNHN) and the National Taiwan Ocean University (NTOU), collected during different oceanographic expeditions carried out in the Indo-Pacific Ocean during the last decades (Table 1). Our sample included 23 of the 26 nominal species of the genus *Paramunida*, plus new undescribed species, as revealed by this study and recognizable on the basis of morphological and sequence data (Table 1). These additional species were designated in the phylogenetic tree with the name of the genus and a number (e.g. *Paramunida sp. 1*). Material from the species *P. spatula*, known from a single specimen in the Austral Archipelago and from *P. antipodes* known from a single collection in Australia could not be obtained. Specimens from *P. hawaiiensis* had been preserved in formalin and failed amplification for all genes. Moreover, during the analysis and writing of this work three new species were discovered so they were not included in the analysis (Cabezas *et al.*, submitted).
In total we gathered 137 individuals. Taxonomic identification was based on morphological characters following the classification key by Baba (2005). To confirm

the taxonomic status of the morphospecies, genetic variation of mitochondrial (ND1, COI and 16SrRNA) and nuclear markers (18S rRNA and 28S rRNA) was examined. Molecular data of the 16S rRNA and COI from previous works (Machordom & Macpherson, 2004; Cabezas *et al.*, 2009) were included in this study (codes Fo and S in the Table 1). These previous data were completed with new sequences for the mitochondrial gene ND1, an extra fragment of the 16S rRNA and the nuclear genes. Two to ten individuals per species were included in the analysis in an effort to cover as much of the geographic range of the species as possible. For species *P. leptotes*, *P. luminata* and three of the phylogenetic undescribed species, only one specimen could be analyzed. Specimens of *P. tricarinata* from Madagascar (*Paramunida sp. 10*) were preserved in formalin and failed to amplify except for a short fragment of the 16S rRNA (436 pb), so they were not included in the final dataset. Nevertheless, independent analysis of this fragment in addition to a morphological study revealed that those specimens from Madagascar should be treated as an independent lineage (see Results). Therefore the final dataset comprised 23 of the nominal species plus 9 phylogenetic undescribed species (*Paramunida sp. 10* not included).

We generated phylogenetic trees for the COI, ND1 and 16S rRNA dataset, and on the basis of these trees we selected a subset of specimens for further sequencing of nuclear markers. The species *Onconida alaini* and *Plesionida concava* were selected as outgroup taxa, since previous works have shown that these two genera are part of the sister clade to the *Paramunida* genus (Machordom & Macpherson, 2004).

DNA amplification and sequencing

Total genomic DNA was isolated from abdominal muscle tissue or pereiopods using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen). In total, five different markers were amplified: two nuclear (28S rRNA and the 18S rRNA) and three mitochondrial (16S rRNA, ND1 and COI) fragments. Amplification was accomplished using either universal or newly designed primers and for the 16S rRNA, 28S rRNA and 18S rRNA genes, two different fragments were amplified (Table 2). Mitochondrial PCR reactions were performed in a final volume of 50 µl, the PCR mix contained 2 µl of DNA template, 0.16 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer (containing a final concentration of 2 mM $MgCl_2$), 0.5 µl of BSA (10 mg/ml), 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. Nuclear PCR reactions were conducted in

50 µl final volume containing 2 µl of DNA template, 0.2 µM of both primers, 0.2 mM of each dNTP, 5µl of buffer without Mg^{++}, 6 µl of 25mM solution $MgCl_2$, 0.5 U of Jump Start Taq DNA polymerase (SIGMA) and ddH_2O. Mitochondrial thermal cycling conditions consisted of an initial denaturation step of 94ºC for 4 min followed by 39 cycles at 94ºC for 30 s, an annealing temperature of 45.5ºC (16S rRNA), 40.5º (ND1) and 45-50º (COI) for 1 min, 72ºC for 1 min, and a final extension at 72ºC for 10 min. Nuclear amplification process included an initial step of 94ºC for 3 min followed by 35 cycles at 94ºC for 30 s, 48-50º (18S rDNA and 28S rDNA, respectively), 72º for 1:30 sec, and a final extension at 72ºC for 7 min. After PCR purification using an ethanol/sodium acetate precipitation (mitochondrial) or the PCR product clean ExoSAP-IT (nuclear), samples were cycle-sequenced using the ABI Prism BigDye Terminator, and subsequently were run on an ABI 3730 Genetic Analyzer (Applied Biosystems, ABI). Sequences are available in GenBank under accession numbers GU814634-GU815088, GU831576-GU831595 and HM060642-HM060644.

Phylogenetic analyses

DNA sequences were edited using Sequencher 4.6 (Gene Codes, Ann Arbor, MI) and aligned manually in Se-Al version 2.0a11 (Rambaut, 1996). The software GBLOCKS (Castresana, 2000) was used to identify ambiguously aligned regions in the 16S rRNA, 18S rRNA and 28S rRNA. Some works have suggested that excluding ambiguous regions may lose phylogenetic information and do not necessarily solve the problem of alignment uncertainty (Wong *et al.*, 2008). To examine the importance of these regions in phylogenetic reconstruction, we run two independent analyses with and without the ambiguous nucleotides. The resulting topologies did not show substantial differences, and in some cases the inclusion of these sites yielded stronger statistical support for several clades. Therefore, these positions were included in the final dataset**.** Phylogenetic reconstructions were performed under Bayesian Inference, maximum likelihood and maximum parsimony methods. Clade support for the MP and ML phylogenies was assessed by non-parametric bootstrapping (Felsenstein, 1985) using 1000 pseudoreplicates and 500 pseudoreplicates, respectively. Bayesian posterior probabilities were used to evaluate the robustness of Bayesian trees. We defined strong phylogenetic support as >70% bootstrap values (Bv) in the MP and ML phylogenetic trees and >95% posterior probabilities (Pp) in the Bayesian ones.

Phylogenies were constructed for each individual marker and congruence among tree topologies was checked looking for conflicting clades with a support greater than 95% Pp or 70% Bv. ModelTest 3.07 (Posada & Crandall, 1998) was used to infer the best molecular evolutionary model for each marker. We used the Akaike's Information Criterion (Akaike, 1974), because this index has been shown to reduce the number of unnecessary parameters by penalizing more complex models (Nylander *et al.*, 2004). Bayesian analyses (BI) were running using the software Mr. Bayes version 3.1.2 (Huelsenbeck & Ronquist, 2001) with two independent runs of four Metropolis-coupled chains with 5000000 generations each. Trees prior to the log likelihood stabilization were discarded as burn-in after assessing run convergence in Tracer v1.4 (Rambaut & Drummond, 2003). To ensure that analyses approached the optimal posterior distribution, an additional run was performed using the same conditions. Parsimony analyses (MP) were performed through a heuristic search with the TBR swapping algorithm, 10 random stepwise additions and treating indels as missing data using PAUP* v4.0 b10 (Swofford, 2002). Maximum likelihood analyses (ML) were conducted in PHYML v2.4.4 (Guindon & Gascuel, 2003) using the evolutionary model selected by ModelTest 3.07, and allowing to the program estimated the model parameters. When the model selected by ModelTest 3.07 was not implemented in PHYML v2.4.4, we used the next best-fitting model, as recommended by the authors.

Estimating times of divergence

To examine the rate constancy of molecular evolution we use the relative rate test (Takezaki *et al.*, 1995) implemented in PHYLTEST 2.0 (Kumar, 1996). After checking that rates did not conform to a molecular clock, a Bayesian relaxed phylogenetic approach implemented in BEAST v1.5.3 (Drummond & Rambaut, 2007) was used to estimate lineage divergence times. Phylogeny and divergence times were estimated using the combined dataset (mitochondrial and nuclear partition). A model GTR+I+G of DNA substitution with four rate categories was implemented for both dataset, pruning species to one single specimen. An uncorrelated normal relaxed molecular clock and the Yule process of speciation were selected as clock and tree prior, respectively. Divergence times were calculated as 95% highest posterior density intervals (HPD) on a chronogram. The 95% HPD is defined as the shortest interval that contains 95% of all values sampled from the posterior.

The fossil record of Decapods, and in particular Galatheidae, is too scarce and biased, to carry out a fossil-based calibration approach (De Grave *et al.*, 2009). Therefore, to obtain absolute divergence times, we calibrated the relative-time chronogram obtained from BEAST using the mitochondrial average rate of molecular divergence proposed for other crustaceans, allowing to the program the estimation of the substitution rate for the nuclear partition. For the 16S rRNA, a mean substitution rate between 0.53% to 0.88% per my has been proposed (Schubart *et al.*, 2000b; Stillman & Reeb, 2001; Lessios, 2008), whereas for genes as variable as COI, a mean divergence value between 1%-2% has been reported (Knowlton & Weigt, 1998; Lessios, 2008). Thus, the BEAST chronogram was calibrated using a normal distribution with a mean of 0.00625 substitutions/site/MY and a standard deviation of 0.0016, using the slowest (0.53% per my) and the fastest (2% per my) substitution rates to avoid placing too much confidence in just one estimate.

Two independent analyses were performed with MCMC chain lengths of $20x10^6$ generations per run. Parameters were logged every 1000 generations. Log files were analyzed using Tracer v1.4 (Rambaut & Drummond, 2003) to examine the effective sample size (ESSs) of each parameter and to determine the appropriate burn-in. After discarding a 10% of the MCMC chains as burn-in, results of the two runs were combined with LogCombiner v1.5.3 to obtain the posterior probability distribution of each parameter and the consensus tree (maximum clade credibility tree with 95% confidence intervals) was compiled with Tree Annnotator v.1.5.3 (Drummond & Rambaut, 2007).

Diversification rates

The maximum-clade credibility tree with absolute ages resulted from the BEAST analysis was used to examine the diversification rates within the group. A relative cladogenesis (RC) test was performed to identify branches with significant increases in diversification rates using the software GEIGER (Harmon *et al.*, 2008) running in R (ver. 2.6.0). This statistic represents the probability that a particular lineage, existing at time t, will have k extant tips under a constant rate birth-death model. Previous studies have shown that tests to identify shifts in diversification rates are sensitive to taxon sampling if 50%, or less than 50%, of the known species have been sampled (e.g. genus *Turbo*, (Williams & Duda, 2008)). Given that we have included more than 80% of the known species in our analyses, our diversification tests could be considered as robust.

To graphically examine the rate of diversification, we plotted the log of the number of lineages against the branch length distance from the root on the ultrametric trees ("lineages-through-time"; LTT) using Genie, ver. 3.0 (Pybus & Rambaut, 2002). LTT plots were tested for significant departures from a constant birth-death model of diversification using the γ-statistic from the Constant Rate test (CR) implemented in Genie (Pybus & Harvey, 2000). Significant gamma values indicate that diversification rates are not constant. Negative values indicate that nodes are closer to the root than expected under a pure birth process (deceleration in the rate of diversification). Positive values indicate that nodes are closer to the tips than expected under a pure birth model (acceleration in the rate of diversification). In these analyses, incomplete taxon sampling can be a source of error, since the CR test can lead to incorrectly rejecting the null hypothesis of constant-rate diversification (Pybus & Harvey, 2000). To explore the effect of missing lineages in *Paramunida*, we used a Monte Carlo Constant Rate test (MCCR) (Pybus & Harvey, 2000), which assumes that incomplete phylogenies contain lineages that are sampled randomly with respect to the complete phylogeny. This test compares the observed value of the gamma statistic against a null distribution of values obtained from random phylogenies generated by simulating the phylogeny to extant diversity and then randomly pruning species to obtain the same size as the actual incomplete phylogeny.

Finally, we also tested three alternative models of lineage accumulation described by (Paradis, 1997), running in R (ver. 2.6.0) the package APE (Paradis *et al.*, 2004) with the option Diversi. Model A assumes a constant rate of lineage accumulation over time (δ). Model B assumes a gradual change in the rate of lineage accumulation, and additionally estimate the parameter β. Values of $\beta<1$ indicate that diversification rates are increasing, whereas values of $\beta>1$ indicate a slow down in diversification. Model C specifies a breakpoint in time (T_c) with two different diversification rates before (δ_1) and after this point (δ_2). Models A is nested in models B and C, but there is no relationship of nestedness between B and C. Therefore a likelihood-ratio test (LRT) was applied to compare model A with B or C. For comparisons between models B and C, the Akaike´s Information Criterion (Akaike, 1974) was used.

Biogeographical analyses

To infer ancestral ranges and biogeographic events that may explain the biogeographic history of *Paramunida*, we used the parametric, maximum likelihood Dispersal-

Extinction-Cladogenesis method developed by Ree *et al.* (2005) and implemented in the program Lagrange version 2.0.1 (Ree & Smith, 2008). Given an organism phylogeny with estimates of branch lengths, the distribution of terminal species, and a transition probability matrix specifying the rate of transition between geographic ranges as dispersal (range expansion) and extinction (range contraction) parameters, Lagrange allows estimating the dispersal and extinction rates and the probabilities of ancestral ranges and range inheritance scenarios using standard maximum likelihood inference algorithms (Ree & Smith, 2009). To date, this method has been only applied to terrestrial organisms (Buerki *et al.,* in press; Clark *et al.*, 2008; Smith, 2009), so this study represents the first attempt to evaluate the usefulness of the method in reconstructing ancestral areas in the marine realm.

In terms of cladogenetic events, there are three alternative range inheritance scenarios (speciation modes): 1) sympatric, the two descendants inherit the one-area ancestral range; 2) allopatric (vicariance), a widespread ancestral range is divided into the two descendants, and 3) peripatric, one descendant inherits one area while the other inherits the entire ancestral range (Ree & Sanmartín, 2009).

Defining the areas of analysis is a critical step in any biogeographic analysis but even more for parametric methods, as these areas represent the foundation on which model states and parameters rest (Ree & Sanmartín, 2009). In oceanic systems, this is even more challenging than in terrestrial scenarios because of the virtual lack of geographical barriers to delimit biogeographic units. Here, we defined seven operational units based on the criteria of sympatry and level of endemism, geographic distance, and geological history among areas: a) Taiwan + Philippines, b) New Caledonia, c) Indonesia, d) French Polynesia, e) Solomon Islands, f) South West Pacific (Vanuatu + Fiji + Tonga + Wallis and Futuna) and g) NE Australia (Fig. 1). For example, even though there are endemic species in each of the South Western Pacific islands (e.g. *P. amphitrita* and *P. curvata*), these islands share a common geological history since they were initially joined into a continuous island arc until the subduction of the Pacific Plate into the Australian Plate occurred during the Oligocene-Miocene boundary (Duffels & Ewart, 1988).

Species was coded according to distribution data from the literature (Baba *et al.*, 2008; Baba *et al.*, 2009) and assigned to one of the seven operational units defined. The alternative approach of using only the collecting site of the sequenced individuals would probably have biased the analysis towards some areas (e.g. New Caledonia or Fiji) that were much better sampled than others.

One drawback (limitation) of parametric methods is that the size of the transition rate matrix (the number of parameters to estimate from the data), increases exponentially with the number of areas, resulting in increased computational times and a loss of resolution power. To solve this, Ree & Sanmartín (2009) suggested to impose geographic structure onto the biogeographic model by limiting the number of possible geographic ranges allowed in the transition matrix. Most species of *Paramunida* are restricted to one or two areas, indicating that gene flow is unlikely across larger ranges. We therefore restricted geographic ranges in the analysis to combinations of one and two-areas. Nevertheless, three and four-area ranges presented in some terminal distributions (Fig. 6) were also implemented into the biogeographic model to allow the convergence of Lagrange (Buerki *et al.,* in press). A common approach in the analysis of terrestrial systems is to disallow disjunct ranges covering areas that are now separated by geographic barriers, since genetic flow would be difficult to maintain across these ranges (Ree & Sanmartín, 2009). Here, we did allow disjunct ranges as possible states in the analysis because area adjacency – the need for areas within ranges to share a physical edge or boundary – does not seem as relevant for marine animals, which are usually good dispersers. This is evidenced by the fact that several species of *Paramunida* did show disjunct ranges, covering areas now separated by ocean stretches of thousands of kilometres (e.g. *Paramunida cristata* distributed in Taiwan and Fiji).

One advantage of Lagrange is its flexibility: dispersal rates in the transition matrix can be constrained (scaled) according to geographic distance or to changes in area connectivity through time, e.g. a land bridge, the rise and low of sea level, marine currents, etc (Ree & Sanmartín, 2009; Sanmartín, 2010). Unfortunately, unlike shallow currents, there is very little data on deep-sea marine currents. We first used an unconstrained DEC model in which dispersal rates among areas were assigned equal probability. Second, we run a DEC analysis in which the dispersal rates between two areas was scaled inversely to the geographic distance to be crossed (Table 3). Thus, the value 1 was assigned to intra-regional dispersal, and 0.01 to the most geographically separated areas (allowing dispersal, but with very low probability). For example, dispersal between South Western Pacific islands and Taiwan-Philippines was considered less likely than between SW Pacific and Australia, and assigned a rate of 0.3 and 0.7, respectively.

RESULTS

Sequence characteristics

The combined mitochondrial dataset yielded a matrix with 1947 characters (575 for the COI, 460 for the ND1 and 912 for the two fragments of the 16S rRNA) (Table 4). The combined dataset (mitochondrial+nuclear) yielded a matrix with 48 taxa and 5527 base pairs with most of the intraspecific variability excluded. A total of 1478 sites were variable, of which 1119 were phylogenetically informative (192 informative sites of 575 bp of included COI, 169/460 bp ND1, 319/912 16S rRNA, 109/1797 18S rRNA and 330/1783 28S rRNA). The mean base frequencies of the mitochondrial genes showed a clear AT bias (69.4% for COI, 78.2% for ND1 and 79.7% for 16S rRNA). Table 4 shows the best fitting-models and parameters associated selected by ModelTest for each dataset.

Phylogenetic reconstruction

Topologies generated for each mitochondrial gene were quite similar (MP, ML and BI), but the independent analysis of the COI marker showed three well supported clades which were not supported by the other two mitochondrial genes. The mitochondrial and combined dataset (mitochondrial + nuclear) were largely congruent, although the combined dataset provided further resolution in the basal nodes and yielded better results of bootstrap values and posterior probabilities than the mitochondrial dataset (Fig. 2 and Fig. 3).

The monophyly of the genus was highly supported in the combined dataset and eight clades were strongly supported, containing three of them just two species (Fig. 3). Relationships within these clades were generally well resolved (e.g. Clade VI or Clade VII), nevertheless relationships of the clades to each other were poorly resolved (Fig. 3). Clade I was the most diverse. Relationshis were well supported in the subclades *Paramunida sp. 5* / *P. tricarinata* + *P. labis*, *P. cretata* + *Paramunida sp. 6*. However, relationships among the different groups were not fully resolved and the phylogenetic position of the species *P. echinata* could not be assessed with confidence. The Clade IV included the species *P. scabra* / *P. evexa*, which were recovered with high support as the sister group of the new species *Paramunida sp. 8*. The clades V, VI and VII were highly supported by all the methodologies. In the first one, the relationship among the species *P. belone* and two recently described species *P. lophia* and *P. salai* was well supported. The new species *Paramunida sp. 4*, morphologically very closely related to

P. belone, was recovered as sister of this group. Within the Clade VII, two subclades were recovered. One including two undescribed species previously assigned to the nominal species *P. setigera* on the basis of morphological characters, and another one including the species *P. longior* plus the new one *Paramunida sp. 3*, both very similar in morphological terms. Finally, the phylogenetic position of the species *P. polita* could not be recovered.

On the other hand, the mitochondrial reconstruction supported seven of these eight clades (Fig. 2), with the exception of the Clade V (*P. amphitrita* / *P. thalie* + *P. curvata*). The monophyly of the group was not statistically supported because the species *P. granulata* was not included as part of the ingroup and relationships at the internal nodes could not be fully resolved.

Species boundaries

Because the mitochondrial analyses covered more individuals from more geographic locations, these were used for species delimitation. Genetic data revealed a total of ten undescribed species which represents an increase of the 38% over the current diversity of the genus. These new taxa can be distinguished by small but consistent morphological differences mainly associated with the spinulation of the carapace, the antennal and antennule peduncle and walking legs (Cabezas *et al.,* submitted). All the new species for which multiple individuals were sequenced were recovered as monophyletic units with high support, satisfying the phylogenetic species concept (Wheeler & Meier, 2000). The specimens of *Paramunida sp. 2* and *Paramunida sp. 3* were so damaged that a careful morphological examination could not be performed. Even though diagnosis characters could not be determined with high confidence, both specimens were treated as different taxonomic units due to the "deep" molecular divergence exhibited in the mitochondrial genes respect to the nominal species where they had been previously assigned (e.g. 4.8% with *P. setigera* and 8.6% with *P. longior* for the COI sequence, respectively). In the case of the *Paramunida sp. 6* only one specimen could be amplified but material from 3 additional individuals could be morphologically analyzed, confirming the constancy of the morphological differences in the new species (Cabezas *et al.,* submitted).

Our results revealed some wide distributed taxa as species-complexes with more restricted distributions. Molecular and morphological analyses revealed as a different lineage specimens of *P. pictura* from French Polynesia. Additionally, our data

supported the existence of a species-complex in *P. setigera*, with different taxa in the Philippines and New Caledonia and adjacent waters, respectively. Finally, specimens of *P. tricarinata* from Madagascar were confirmed as a different taxonomic unit (*Paramunida sp. 10*) on the basis of monophyly showed by the solely fragment of the 16S rRNA analyzed (data not shown), molecular divergence values respect to the nominal species *P. tricarinata* and morphological differences (Cabezas *et al.,* submitted). Finally, we recovered a phylogeographic pattern for those species where a good population sampling was obtained (Fig. 2, e.g. *Paramunida sp. 1*, *P. stichas* and *P. proxima*).

Mitochondrial intraspecific sequence divergence ranged from 0% to 1.53% and the interspecific distance within clades ranged from 1.56% to 21.06% (Table 5). No overlapping between the intra and interspecific values was reported, and the mean divergence values were in this range COI~ND1>16S rRNA.

Timing and tempo of diversification

A chronogram representing acceleration in diversification rate and divergence times is showed in Fig 4. Five significant increases in diversification rates were identified within the *Paramunida* phylogenetic reconstruction. The first three diversification increases corresponded with well supported deep nodes (RC test $P_{RC1} = 0.00073$, RC test $P_{RC2} = 0.0014$ and RC test $P_{RC3} = 0.0108$) and showed a mean age estimate of 20.66 Ma (13.02-33.2 Ma), 19.39 Ma (12.61-31.97 Ma) and 19.22 Ma (12.05-30.45 Ma), respectively (Fig. 4). The fourth event corresponded with a not well supported clade ($P_{RC4} = 0.0157$) and showed a timing of diversification with a mean divergence time of 17.05 Ma (11.47-29.46 Ma). Finally, an acceleration of the diversification rate was identified approximately 10 Ma (RC test $P_{RC5}=0.0481$).

The origin of the *Paramunida* genus lied within the Miocene; however, large 95% HPD intervals suggested that the pulse of speciation could have occurred even earlier, during the Oligocene. The species *P. granulata* appeared to undergo an early split but the Pp of this node was lower than 50% and therefore 95% HPD bars could not be estimated.

The lineage-through-time plot (LTT) for the phylogeny of *Paramunida* was convex and differed significantly from a constant rate of diversification (speciation-extinction) over time (Fig. 5). This result suggested an early burst of speciation, but in order to test if this finding was indicative of a real rapid speciation process or if it was an artefact because of incomplete taxon sampling, the γ statistic was calculated ($\gamma = -2.69$). The

MCCR test showed a critical value of γ at $P = 0.05$, one-tailed test, $\gamma_{0.05} = -1.90$ (species sampled, x = 32; estimated total number of species, y = 39). Finally, the survivorship analyses suggested that Model B (gradual change in the rate of lineage accumulation) with a β value of 1.73 fitted the data better than a constant rate model (Model A) or a model with two distinct rates of diversification (Model C). All these evidences would support that *Paramunida* squat lobster genus underwent an early pulse of speciation in the Oligocene-Miocene boundary followed by a slowdown in the rate of lineage accumulation over the time.

Biogeographical reconstruction

The Lagrange unconstrained (Fig. 6) and the Lagrange geographically-constrained analysis (Fig. 7) gave very similar results, for both reconstructed ancestral area ranges and estimates of dispersal and extinction rates. Dispersal rates were slightly higher for the constrained model (*d* unconstrained = 0.03196, *d* constrained = 0.08776), whereas extinction rates were very similar for both models (*e* unconstrained = 0.02785, *e* constrained = 0.0265). The model likelihood was significantly higher for the unconstrained model (-lnL = 122.3) than for the constrained model (-lnL = 134.6), indicating a better fit to the data for the former model, in which dispersal rates are not dependent on geographic distance. In general, dispersal rates were unexpectedly high for a genus whose species are so geographically restricted: *d* = 0.03196/0.08776, especially if we compare it with other published plant studies (*d* = 0.009, Buerki *et al.*, in press). The phylogeny shows that even though many species are endemic to one area, most of them have their sister-group in a different area (e.g. *Paramunida setigera* - *Paramunida sp. 2*). There are no monophyletic clades of three or more species within the same area, and few speciation events within single-areas (e.g. *Paramunida salai* - *Paramunida lophia*). There are also few cases of vicariance or allopatric speciation (e.g. *Paramunida belone* - clade *Paramunida salai* - *lophia*). In contrast, peripatric speciation, in which one species is present along the entire ancestral range and its sister is restricted to a small part of it, seems to be the common speciation mode in this group (e.g. *Paramunida stichas* - *Paramunida proxima*). Interestingly, branches separating internal nodes (internodes) are relatively long, indicating long time available for dispersal, which would explain the high dispersal rate. However, this can be also an artefact produced by incomplete taxon sampling, since missing species could shorten the time between

speciation events and lower the dispersal rate if all missing branches (species) occur within the same area.

The maximum likelihood DEC reconstruction indicated that the ancestor of genus *Paramunida* was restricted to the South Western Pacific area, covering the island arc formed by Fiji, Samoa, Tonga, Vanuatu, Wallis and Futuna. Thus, this region could have been the ancestral area of the genus. From the SW Pacific region, *Paramunida* ancestors dispersed to the north and east, colonizing Australia, New Caledonia, the Solomon Islands, the French Polynesia and the South East Asia continental areas (Taiwan, Philippines and Indonesia). Dispersal to Taiwan -Philippines (area a) seems to have occurred independently at least twice: in the lineage leading to the clade *Paramunida sp. 1* - *Paramunida setigera* / *Paramunida sp. 2* (a/af) and along the clade formed by *Paramunida sp. 5* /*Paramunida tricarinata – Paramunida labis* (a/f). Colonization of Indonesia (area c) seems to have occurred via New Caledonia (area b) (e.g. MRCA of clade *Paramunida sp. 8* / *Paramunida evexa -scabra*). Colonization of the French Polynesia (area d) took place only once in the ancestor of the clade *Paramunida pictura* - *Paramunida sp. 7*.

DISCUSSION

An incomplete taxon sampling is almost an unavoidable source of error and this issue is more striking for marine species distributed in deep-sea strata since vast areas in the ocean are poorly explored. This work represents a novel contribution to understand the diversification and biogeography of deep marine fauna in the Pacific; however, it is necessary to keep in mind the drawback imposed by our taxon sampling in order to establish the limits of our interpretations.

Classification and phylogeny of *Paramunida*

This study has added ten new taxonomic units to the 26 previously described species (Baba *et al.*, 2008), which represents an increase in species diversity by 38%. During the last decades, the extensive application of molecular tools in systematic studies have pointed out how the number of described morphospecies tends to be an underestimation of the real diversity in many marine taxa (Meyer, 2003; Malay & Paulay, 2009).

Much of this incongruence reflects the lack of taxonomic studies, but also the difficulty to identify diagnostic characters and determine the intraspecific variability in groups where the homoplasy of the morphological characters is high.

Here, although the *Paramunida* genus has received great taxonomical attention during the last decades (Baba, 1988; Macpherson, 1993; Macpherson, 1996), the high morphological similarity among lineages makes very difficult species delimitation. Convergence or stasis in the morphological evolution seems to be a common phenomenon within decapods (Knowlton, 1986; Schubart *et al.*, 2000a). It has been proposed that extreme environmental conditions can lead a stabilizing selection on morphology, reducing or even eliminating the morphological change that can accompany the cladogenesis process (Bickford *et al.*, 2007). Within the family Galatheidae, approximately 85% of the species are linked to deep waters and it can be hypothesized that the homogeneity and stability of those habitats could have entailed the selection of similar morphotypes. However, cryptic speciation has also been described in galatheids associated with shallow waters (Cabezas *et al.*, 2010), suggesting that the high morphological similarity must be more related with the evolutionary history of the group rather than with a limitation imposed by the habitat.

At phylogenetic level, the uncertain position of the species *P. granulata* disputes the monophyly of the genus in the mitochondrial reconstruction (Fig. 2), while the nuclear data (not shown) and the combined dataset recovered the genus as monophyletic (Fig. 3). This discrepancy could be result of an early split of this species. Although the monophyly of the genus was not well supported by the bayesian coalescent approach and therefore 95% HPD were not estimated, it seems clear that species underwent an early separation, probably dating back to the Upper Oligocene (Fig. 4). Morphologically *P. granulata* is characterized by having a very long distomesial spine in the second article of the antennal peduncle, which is clearly shorter in the rest of species of the genus (Baba, 1988). This conspicuous morphological difference in addition to high values of molecular divergence and its widespread distribution suggest that this species could belong to another genus. In the present work, we do not make a formal decision about raising the species to a higher taxonomic status until more material can be analyzed.

Timing and causes of diversification

The origin and causes involved in marine diversification in the Indo-Pacific region have been extensively debated (Barber, 2009 and references cited herein). Early studies showed sea level changes and climatic oscillation during the Pliocene-Pleistocene glaciations as the driving force responsible for the high species diversity peak observed in the area (Benzie & Williams, 1997). However, more recent works using an approach

of calibrated molecular phylogenies with fossils did not show evidence for species level radiations during the last 3 Ma (Williams & Reid, 2004; Barber & Bellwood, 2005), otherwise supported an older diversification from Oligocene onwards (Williams, 2007; Williams & Duda, 2008; Malaquías & Reid, 2009). The intense tectonic activity during the Oligocene-Miocene period has been erected as the main factor promoting such rapid increases in diversification rates (Renema *et al.*, 2008; Williams & Duda, 2008), which may augmented the geological complexity in the region providing new opportunities for the isolation and diversification of marine species (Wilson & Rosen, 1998).

The impact of such process on species associated with coral-reef systems or shallow waters seems unquestionable, but its effect on faunas associated with deeper waters remains unclear (Williams & Duda, 2008; Malaquías & Reid, 2009). Previous works based on deep sea squat-lobster of the genus *Munida* reported a significant increase in diversification rates during the same period proposed for other shallow water taxa (Machordom & Macpherson, 2004). Moreover, a very recent study focused on the biogeographic patterns of deep-sea galatheids in the Pacific suggested that similar evolutionary and ecological processes may have affected both shallow and deep-water faunas (Macpherson *et al.*, 2010).

In agreement with these results, our study hold up a rapid pulse of speciation for squat-lobsters of the *Paramunida* genus over a narrow period time between the Oligocene-Miocene, followed by a decrease in the rates of lineage accumulation. Divergence time estimates showed in this study should be regarded cautiously since 95% HPD intervals were large and overlapping. As has been proposed, the most presumable process promoting this rapid cladogenesis it is the intense tectonic activity during that period. Plate-tectonic reorganization may increased oceanic volcanism and the formation of islands (Neall & Trewick, 2008), offering new opportunities for colonization and disruption of genetic flow; and modulating the area and suitability in both shallow and deep sea environments (Renema *et al.*, 2008; Williams & Duda, 2008). These events probably resulted in an increase of suitable habitats for squat-lobsters, which were filled in a short period of time, certainly providing an excellent scenario for a rapid speciation process. It has been proved that the availability of new niches allowed the expansion of shallow water ecosystems such sea grasses and reefs, promoting the diversification of associated taxa (Alfaro *et al.*, 2007; Teske & Beheregaray, 2009). Some squat-lobsters, *Paramunida* genus among them, are occasionally recorded living in association with sessile organisms (e.g. gorgonians, sponges and corals) but this fact does not seem to

represent a key factor in determining the presence/absence of the species (Kilgour & Shirley, 2008; Rowden *et al.*, 2010). Most squat-lobsters are not linked to specific habitats, inhabiting rocky, sandy or muddy substrata indistinctly (Zainal, 1990). Although it is difficult to envisage how the intense tectonic activity during the Oligocene-Miocene modulated the suitability of deep-sea habitats, our divergence estimations would support a causal linkage between squat-lobsters species radiation and tectonics.

In addition, alternative processes such as climatic shifts, changes in oceanic currents and speciation-extinction dynamics have also been argued to be crucial in diversification of Indo-Pacific marine faunas (Reaka *et al.*, 2008). Evaluating the effect of historical alterations in oceanic circulation is impossible, but evidence has revealed its important role in relation with connectivity and disruption of gene flow among marine populations (Barber *et al.*, 2002; Connolly *et al.*, 2003). On the other hand, the onset of an overall warming during that period could also affect the rates of diversification, since high temperatures seems to be related with an acceleration of speciation rates (Allen *et al.*, 2006; Williams, 2007). Finally, the absence of fossil record makes difficult to evaluate the role of extinction in the diversification of the *Paramunida* genus (De Grave *et al.*, 2009). Pliocene extinctions in reef-associated species have been reported in the western Atlantic and eastern Pacific (Vermeij, 1989), mainly in association with sea-level changes. Nevertheless, the impact of this factor in faunas distributed below 200 m must have been irrelevant, since the lowest sea-level reach a maximum of 100-150 m respect to the present level. Instead of, both abrupt palaeoceanographic changes and deep-sea warming have been proposed as the main causes to explain extinctions in deep marine benthic foraminifers (Kennett & Stott, 1991). Although we could not be addressed the role of extinction, our results supported an initial diversification marked by higher speciation rates than extinction ones where the group may reached the maximum diversity, followed by a period with similar speciation and extinction rates.

This study adds strong evidence for a common period of diversification in both shallow and deep-sea environments during the Oligocene-Miocene in the West Pacific; nonetheless complementary data from other deep water taxa would be desirable in order to confirm this pattern. A better taxon sampling, an increasing geographical resolution in combination with more accurate substitution rates will allow us to make more precise inferences about the origin and processes involved in galatheid diversification.

Biogeographical reconstruction and species distribution

The generation of marine diversity in the Indo-Pacific Ocean has attracted the interest of evolutionary biologists since the times of Charles Darwin (Wallace, 1860; Wallace, 1881). The integration of new model-based biogeographic methods in combination with time-calibrated molecular phylogenies has promises to improve our knowledge on the processes that generated such an amazing biodiversity (Barber, 2009). Newly developed parametric methods for biogeographical reconstruction allow the integration of new sources of external evidence to biogeographic inference, such as those from the fossil record, plate tectonics, or paleoclimate reconstructions, thus allowing us to test increasingly complex biogeographic models and hypotheses (Ree & Sanmartín, 2009; Smith, 2009). Furthermore, these methods have proven to be useful to explore biogeographic hypotheses even, when as in the present study, there are large confidence intervals associated to divergence time estimation and uncertainty in phylogenetic relationships (Smith, 2009).

The Dispersal-Extinction-Cladogenesis model (Ree & Smith, 2008) has evidenced its usefulness to reconstruct biogeographic patterns in terrestrial organisms, both continental and insular (Clark *et al.*, 2008; Santos *et al.*, 2009; Smith, 2009), representing this study the first attempt to apply it to the marine realm, with its vertical, non-horizontal zonation and unclear boundaries between biogeographic units.

Our study points to the region of the SW Pacific, specifically the island arc of Fiji, Samoa, Tonga, Vanuatu and Wallis and Futuna (marking the margin of the Indo-Pacific-Australian plates), as a centre of diversification for *Paramunida* genus. This result partially agrees with a previous work where multiple centres of diversification were identified for deep-sea galatheids in the Pacific – SW Pacific, Indo-Malay-Philippines archipelago (IMPA), New Zealand and French Polynesia- on the basis of species richness and endemicity of 22 genera (Macpherson *et al.*, 2010).

Here, the lack of evidence to support the existence of independent centres of diversification in the Pacific could be associated with a biased in sampling effort. Most of *Paramunida* species are mainly distributed in the region of the SW Pacific (Baba *et al.*, 2008); however, further exploration in the West Pacific region is necessary in order to obtain more accurate distributional data. Despite general limitations imposed by taxon sampling: 1) the high degree of endemicity in the SW Pacific, 2) the lack of monophyletic clades including three or more species within the same area and 3) sister group species distributed in different areas, makes conceivable the existence of a centre

of speciation in the SW Pacific and highlights the role played for the area in the diversification of the group. Our results suggest that given enough time, squat lobsters of *Paramunida* genus can colonize areas separated by long ocean distances. So, presumably *Paramunida* ancestors diversified in the SW Pacific as a result of intense volcanism, as well as abrupt palaeoceonagraphic changes and the onset of overall warning occurred during the Oligocene-Miocene in the margin of Indo-Pacific-Australian plates (Duffels & Ewart, 1988), with a subsequent dispersion to other Pacific regions.

On the other hand, our results emphasize that geographic distance is not a good criterion to model dispersal rates in marine organisms, as evidenced by the fact that the unconstrained dispersal model showed a better fit to the data than the constrained one (restriction rates to dispersal were applied to geographic distances). Albeit the duration of the larval stages is expected to correlate with dispersal abilities and thus with species distributions, recent works suggest that both life-history traits are weakly correlated (Paulay & Meyer, 2006; Lester *et al.*, 2007; Macpherson & Raventos, 2007). So, alternative factors such as larval retention, adult behaviour, small-scale hydrographic variability and oceanographic currents are now proposed to have stronger influence on the structure of marine populations than dispersal capabilities (Cowen *et al.*, 2000; Reaka *et al.*, 2008; Galarza *et al.*, 2009).

For deep-sea organisms, as squat-lobsters, the presence of deep basins or tectonic trenches at subduction zones seems to represent potential geographic barriers constraining the dispersal. Adult stages of *Paramunida* species usually live between 200 and 500 m (Macpherson *et al.,* 2010), which means that deep-sea trenches, such as those that separate New Caledonia from the island arc of Fiji, Samoa, Tonga, Vanuatu and Wallis and Futuna, could represent insurmountable barriers for the dispersal of species. At the same time, the phylogeographic pattern recovered for some species (e.g. *Paramunida sp. 1*) would support the idea that Fiji, Tonga,Vanuatu and Wallis & Futuna are a geological continuum (geographic) since there is very little geographic structure (genetic distances are small between the three island-endemic populations). The only exception is Tonga-Fiji species pair (*P. cretata – Paramunida sp. 6*), for which genetic distances are much longer (similar divergence levels as other species pairs) so they were delimited as different taxonomic units. All these evidences would support the idea of delimiting biogeograpic units for deep-sea organisms based on geology-paleogeographic criteria.

CONCLUSIONS

This study has uncovered a large amount of hidden diversity within the deep-sea genus *Paramunida*, with an increase in species diversity by 38%. Our results emphasize the importance of the SW Pacific area as a center of diversification in galatheids, which is probably related high tectonic activity, abrupt palaeoceonagraphic changes and deep-sea warming in this region, following the collision of the Australian and Pacific Plates at the Oligocene-Miocene boundary. The existence of a rapid pulse of speciation for *Paramunida* genus adds strong evidence for the existence of a common period of rapid diversification in both shallow and deep-sea environments. We also show how the geographic distance is not a relevant barrier in marine deep-sea organisms, as evidenced by the fact that the unconstrained dispersal model fit better the data than the constrained one. Probably, alternative factors as geographic barriers associated to plate trenches, oceanographic currents or larval retention can be more decisive. We present the first attempt to unravel the origin and diversification of a deep water lineage in Pacific waters. However, it is possible that, with the addition of more taxa and an improvement of distributional data, a better framework will emerge to understand the evolutionary process in deep waters.

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FIGURE LEGENDS

Figure 1. Distribution of *Paramunida* species studied and operational units defined to perform biogeographical analyses (black squares).

Figure 2. Majority-rule-consensus from a Bayesian analysis of the mitochondrial dataset (16S rRNA, COI and ND1). The values above the branches represent parsimony and maximum likelihood bootstraps (Bv) respectively and the values below the branches represent Bayesian posterior probabilities (Pp). Asterisks represent well supported clades within the same species.

Figure 3. Bayesian phylogenetic tree constructed using mitochondrial and nuclear concatenated genes. The values above the branches represent parsimony and maximum likelihood bootstraps (Bv), respectively and the values below the branches represent Bayesian posterior probabilities (Pp).

Figure 4. Chronogram with branch lengths proportional to time (Mya) estimated with a Bayesian relaxed clock approach (BEAST) on the combined dataset and calibrated with the average mitochondrial molecular rate. Clades with significantly increased rates of diversification are indicated by thick black lines and symbols indicate levels of significance using the relative cladogenesis test (++ $P<0.01$ and + $P<0.05$). Asterisks below branches represents clades supported by Bayesian analysis ($Pp>95$), grey bars represent 95% highest posterior density (HPD) intervals and numbers correspond with mean age estimate.

Figure 5. Lineage-through-time-plot (LTT) for genus *Paramunida* based on the chronogram in Fig. 4 and showing the increased rate of diversification at the Oligocene-Miocene boundary. The dotted line represents a constant rate of diversification over time.

Figure 6. Reconstruction of the biogeographic history of *Paramunida* inferred using the Dispersal-Extinction-Cladogenesis model (DEC) implemented in Lagrange (Ree & Smith, 2008). The tree is the maximum-clade-credibility tree from BEAST. Pie charts at nodes represent ML relative probabilities for range inheritance scenarios: a) Taiwan + Philippines, b) New Caledonia, c) Indonesia, d) French Polynesia, e) Solomon Islands, f) South West Pacific (Vanuatu + Fij i+ Tonga + Wallis and Futuna) and g) NE Australia. The white colour represents the reconstruction with the highest relative probability; red and blue represent, respectively the second and third most likely inferred reconstructions. Alternative reconstructions with a relative probability below 0.01 are represented by the black colour. Code letter behind species name correspond with current distribution.

Figure 7. Biogeographical reconstruction of *Paramunida* inferred using Lagrange with a constrained model in which dispersal rates are scaled by geographic distance. See Fig. 6 for abbreviations and other conventions.

TABLE LEGENDS

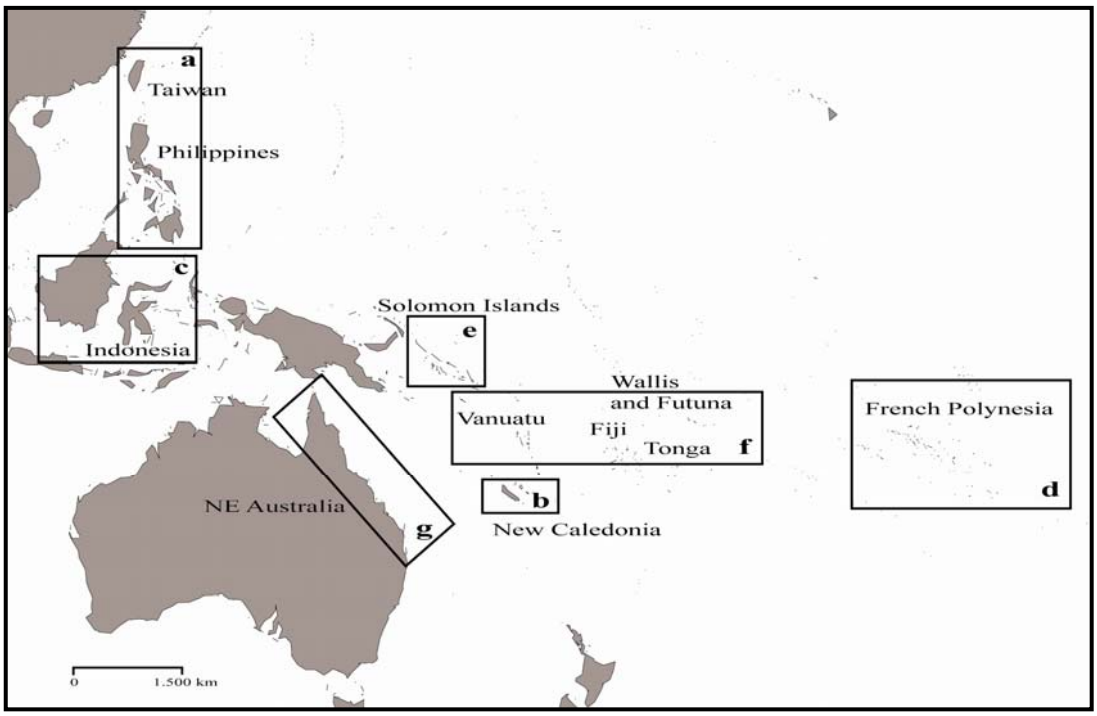
Table 1. Species and gene sequences included in the analysis. *Specimen PAR51 failed the amplification of the second fragment of the 18S rRNA, PAR75-76-77 only could be amplified for the first fragment of the 16S rRNA and specimen PAR123 failed to amplify the second fragment for both nuclear genes.

Table 2. Loci and primers used in this study to amplify and sequence mitochondrial and nuclear genes.

Table 3. Dispersal rates between areas. See text for correspondence between letter code and areas.

Table 4. Mitochondrial, nuclear and combined datasets including informative sites and maximum likelihood models selected through AIC criterion as implemented in ModelTest. Base frequencies, rate matrix, gamma shape parameter and proportion of invariable sites are showed.

Table 5. Average intra and interspecific divergence among *Paramunida* species.



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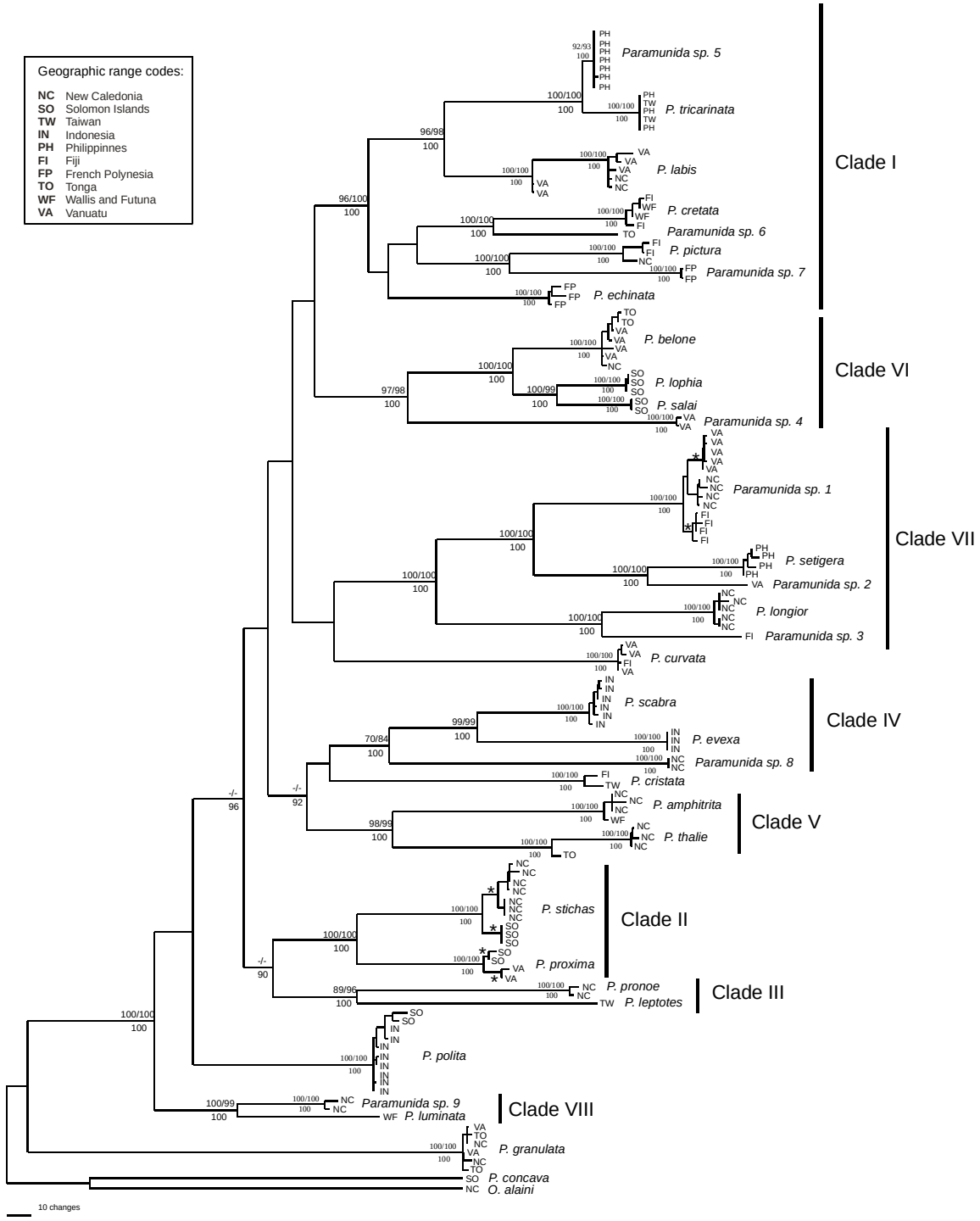

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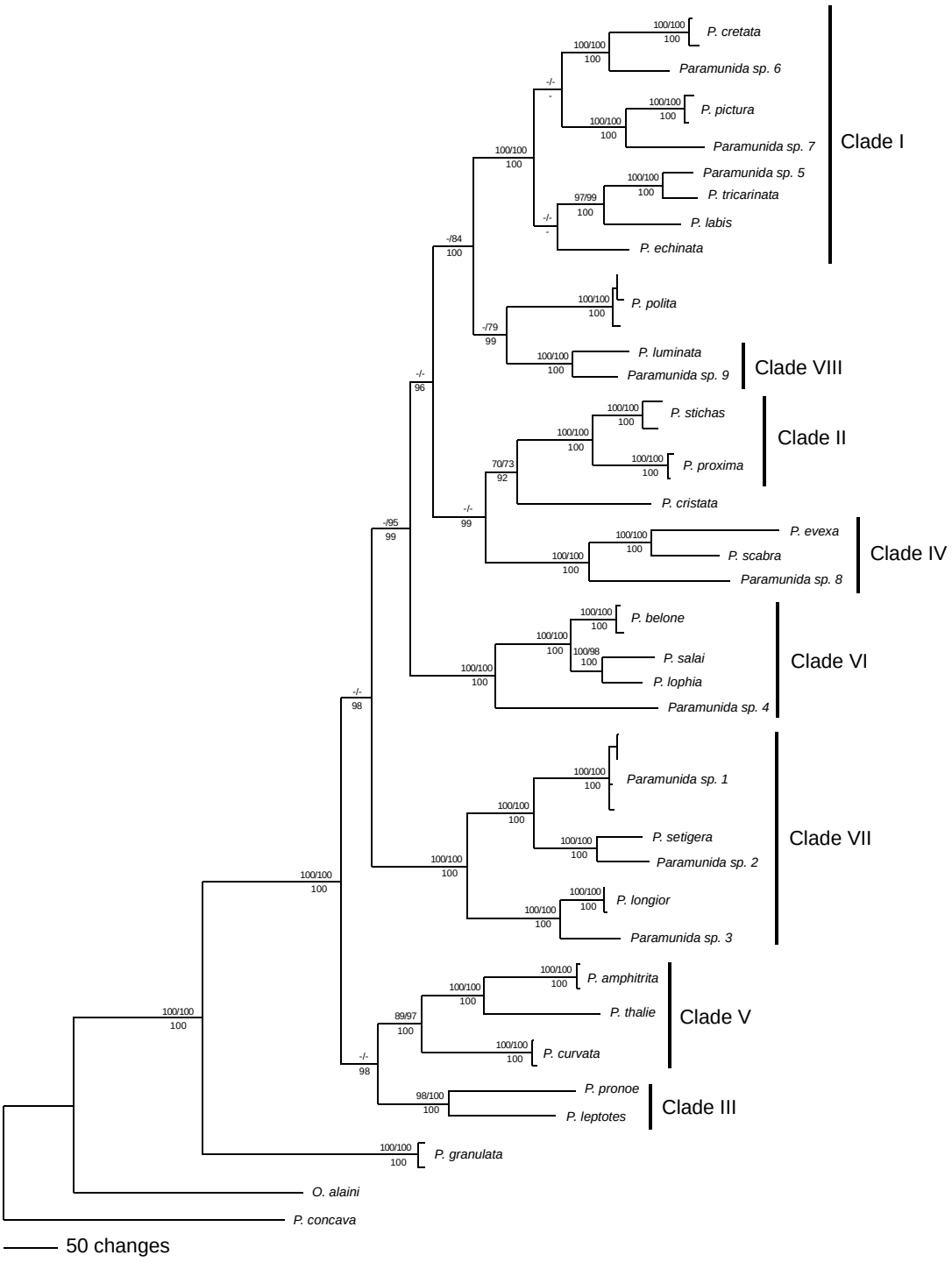

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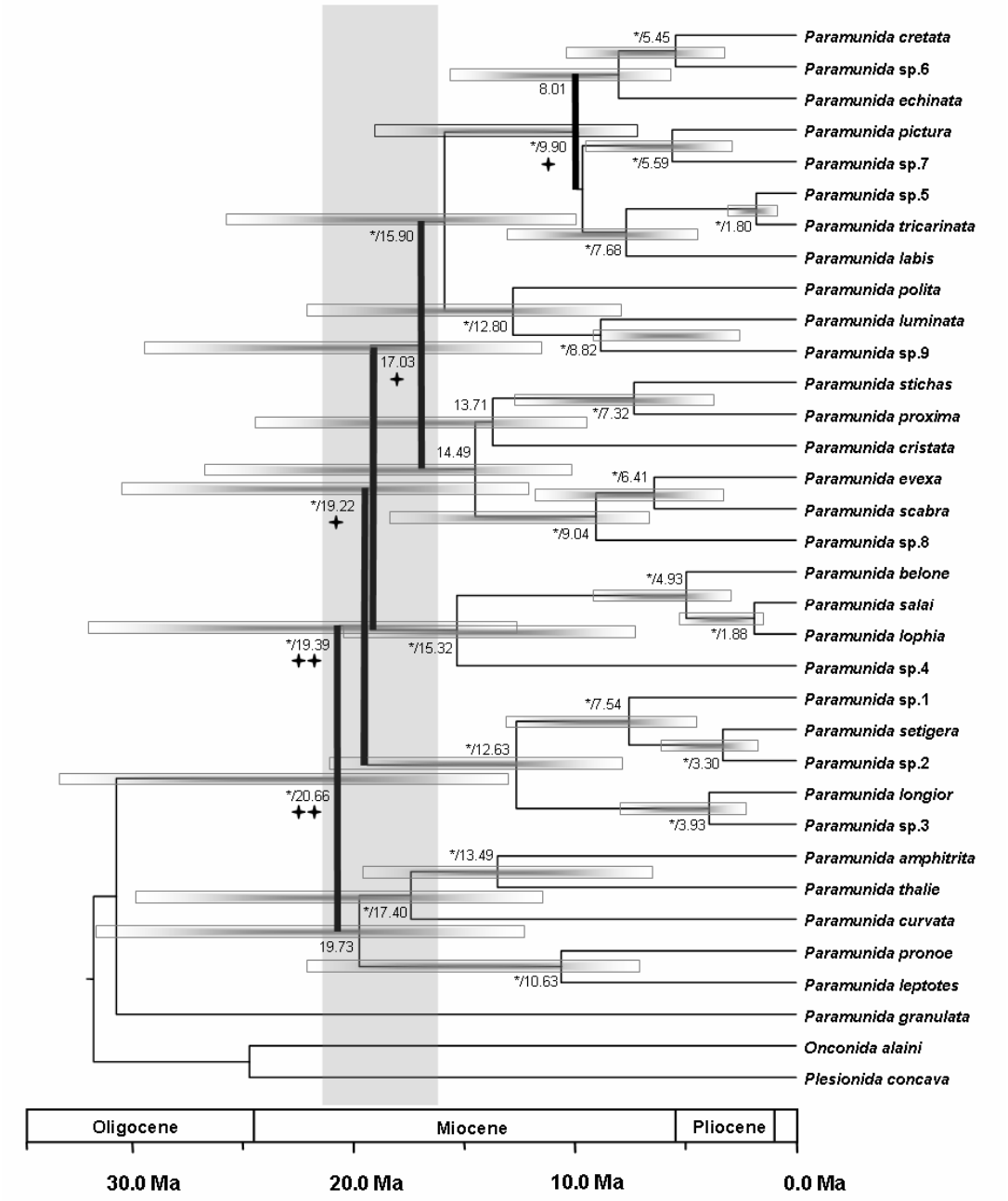

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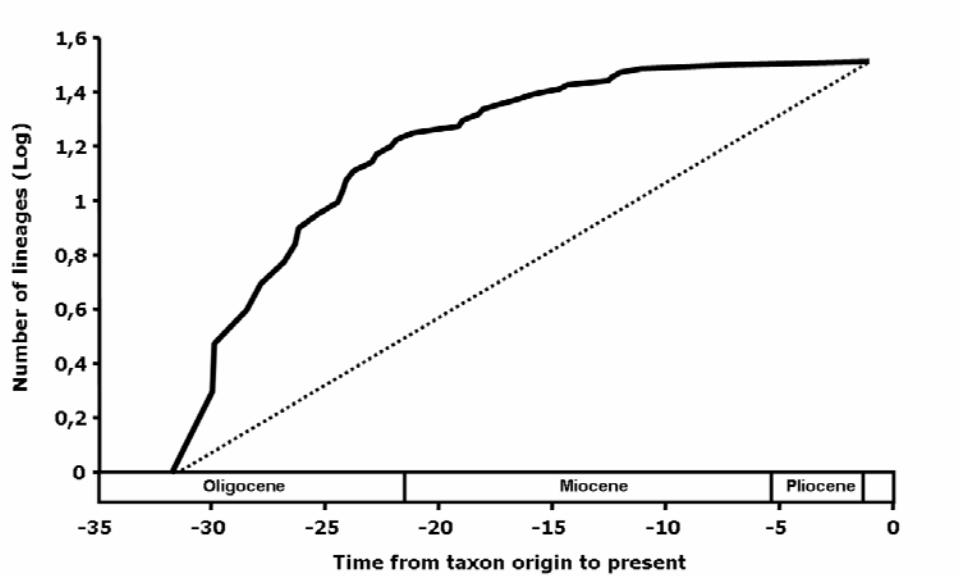

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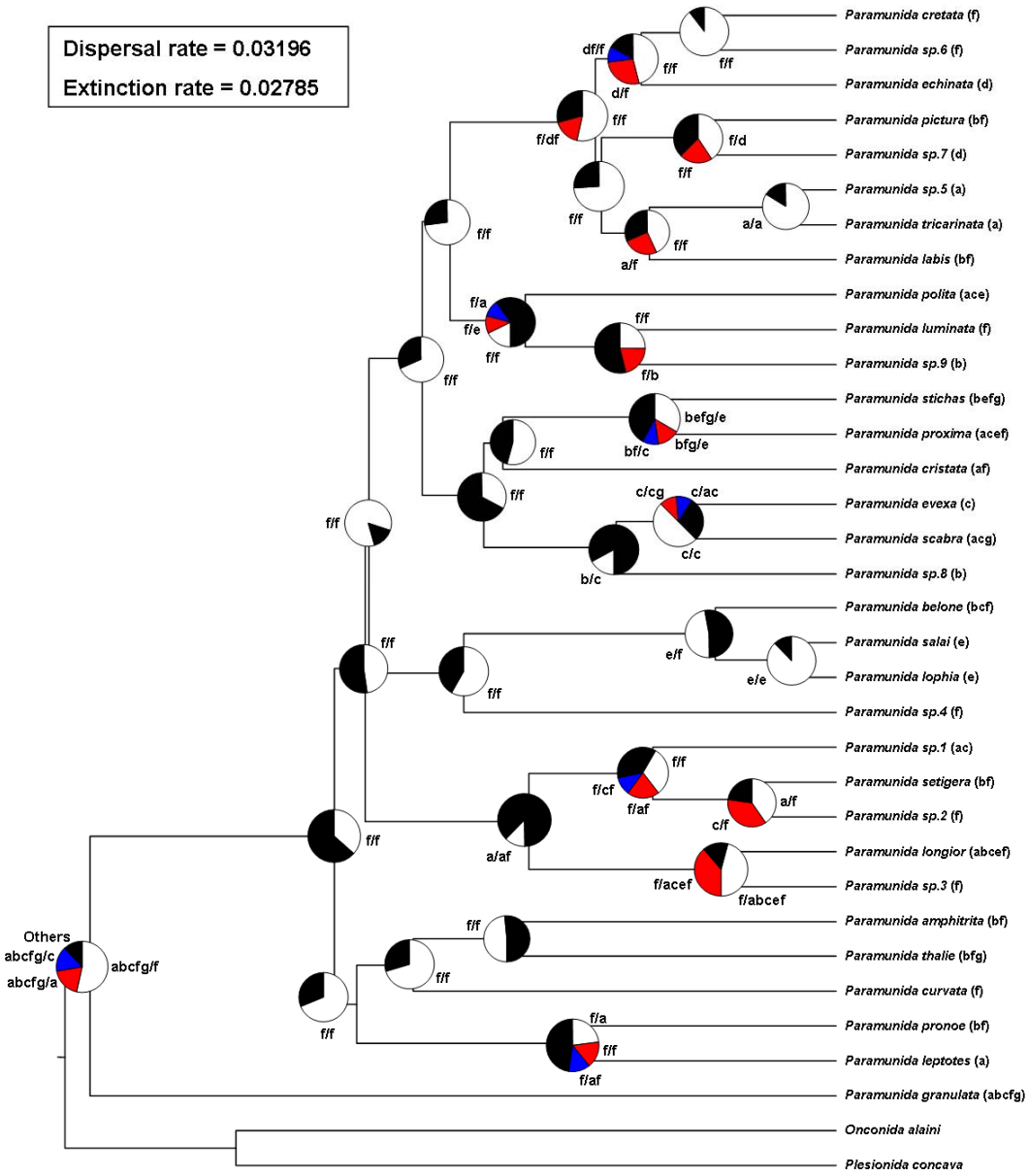

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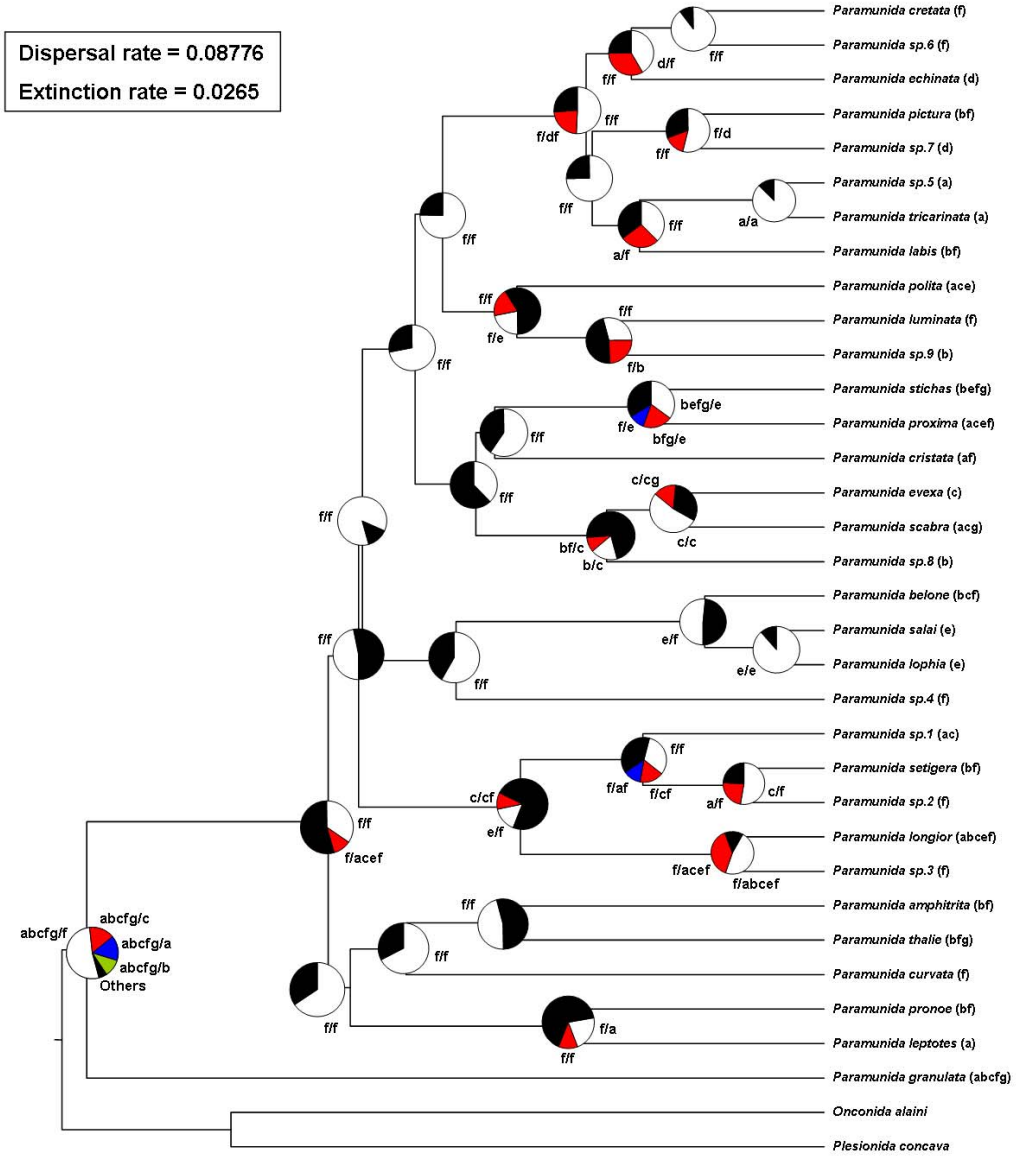

Figure 7. Biogeographical reconstruction of *Paramunida* inferred using Lagrange with a constrained model in which dispersal rates are scaled by geographic distance. See Fig. 6 for abbreviations and other conventions.

Code	Species	Geographic region	Survey	Station	Depth (meters)	COI	16S	ND1	18S	28S
Fo191	*Onconida alaini*	New Caledonia	NORFOLK 1	CP1670	382-386	X	X	X	X	X
S8	*Plesionida concava*	Solomon Islands	SALOMON 2	CP 2260	399-427	X	X	X	X	X
PAR1	*Paramunida amphitrita*	Wallis and Futuna	MUSORSTOM 7	CP 517	233-235	X	X	X	X	X
PAR3	*Paramunida amphitrita*	New Caledonia	LIFOU	DW 15	120-250	X	X	X	X	X
PAR9	*Paramunida amphitrita*	New Caledonia	LIFOU	DW 15	120-250	X	X	X		
PAR11	*Paramunida amphitrita*	New Caledonia	LIFOU	DW 15	120-250	X	X	X		
PAR71	*Paramunida belone*	Vanuatu	MUSORSTOM 8	CP 963	400-440	X	X	X		
PAR72	*Paramunida belone*	Vanuatu	MUSORSTOM 8	CP 963	400-440	X	X	X		
PAR73	*Paramunida belone*	Vanuatu	MUSORSTOM 8	CP 963	400-440	X	X	X	X	X
PAR74	*Paramunida belone*	Vanuatu	MUSORSTOM 8	CP 963	400-440	X	X	X		
PAR129	*Paramunida belone*	Tonga	BORDAU 2	CP 1511	384-402	X	X	X	X	X
PAR130	*Paramunida belone*	Tonga	BORDAU 2	CP 1511	384-402	X	X	X		
Fo196	*Paramunida belone*	New Caledonia	NORFOLK 2	CP 1719	245-437	X	X	X		
PAR7	*Paramunida cretata*	Wallis and Futuna	MUSORSTOM 7	DW 569	300-305	X	X	X	X	X
PAR20	*Paramunida cretata*	Fiji	BORDAU 1	CP 1412	400-407	X	X	X		
PAR21	*Paramunida cretata*	Fiji	BORDAU 1	CP 1412	400-407	X	X	X	X	X
PAR99	*Paramunida cretata*	Wallis and Futuna	MUSORSTOM 7	DW 569	300-305	X	X	X		
PAR6	*Paramunida cristata*	Fiji	BORDAU 1	CP 1447	420-513	X	X	X		
PAR156	*Paramunida cristata*	Taiwan	TAIWAN (NTOU)	CP 269	397-399	X	X	X	X	X
PAR8	*Paramunida curvata*	Fiji	MUSORSTOM 10	CP 1389	241-417	X	X	X	X	X
PAR145	*Paramunida curvata*	Vanuatu	BOA 0	CP 2326	260-313	X	X	X		
PAR146	*Paramunida curvata*	Vanuatu	BOA 0	CP 2326	260-313	X	X	X	X	X
PAR147	*Paramunida curvata*	Vanuatu	BOA 0	CP 2326	260-313	X	X	X		
PAR52	*Paramunida echinata*	Marquesas Islands	MUSORSTOM 9	CP 1176	200-260	X	X	X		
PAR53	*Paramunida echinata*	Marquesas Islands	MUSORSTOM 9	CP 1176	200-260	X	X	X		
PAR54	*Paramunida echinata*	Marquesas Islands	MUSORSTOM 9	CP 1176	200-260	X	X	X	X	X
PAR49	*Paramunida evexa*	Indonesia	KARUBAR	CP 86	223-225	X	X	X		
PAR50	*Paramunida evexa*	Indonesia	KARUBAR	CP 86	223-225	X	X	X		
PAR51	*Paramunida evexa*	Indonesia	KARUBAR	CP 86	223-225	X	X	X	X*	X
PAR27	*Paramunida granulata*	New Caledonia	MUSORSTOM 6	DW 468	600	X	X	X		
PAR86	*Paramunida granulata*	Vanuatu	MUSORSTOM 8	CP 1027	550-571	X	X	X		
PAR88	*Paramunida granulata*	Vanuatu	MUSORSTOM 8	CP 1027	550-571	X	X	X		
PAR126	*Paramunida granulata*	Tonga	BORDAU 2	CP 1640	564-569	X	X	X	X	X
PAR127	*Paramunida granulata*	Tonga	BORDAU 2	CP 1640	564-569	X	X	X		
Fo106	*Paramunida granulata*	New Caledonia	NORFOLK 2	CP 1694	400-650	X	X	X	X	X
PAR28	*Paramunida labis*	Vanuatu	MUSORSTOM 8	CP 971	250-315	X	X	X		
PAR29	*Paramunida labis*	Vanuatu	MUSORSTOM 8	CP 971	250-315	X	X	X	X	X
PAR30	*Paramunida labis*	Vanuatu	MUSORSTOM 8	CP 971	250-315	X	X	X		
PAR40	*Paramunida labis*	Vanuatu	MUSORSTOM 8	CP 1025	335-410		X	X		
PAR41	*Paramunida labis*	Vanuatu	MUSORSTOM 8	CP 1025	335-410		X	X		
Fo64	*Paramunida labis*	New Caledonia	NORFOLK 1	CP 1683	245-440	X	X	X		
Fo151	*Paramunida labis*	New Caledonia	NORFOLK 2	CP 1718	245-440	X	X	X		
PAR154	*Paramunida leptotes*	Taiwan	TAIWAN (NTOU)	CP 380	329-456	X	X	X	X	X
PAR37	*Paramunida longior*	New Caledonia	HALIPRO 1	CP 864	430	X	X	X		
PAR38	*Paramunida longior*	New Caledonia	HALIPRO 1	CP 864	430	X	X	X	X	X
PAR46	*Paramunida longior*	New Caledonia	BATHUS 2	CP 742	362-470	X	X	X	X	X
PAR47	*Paramunida longior*	New Caledonia	BATHUS 2	CP 742	362-470	X	X	X		
PAR48	*Paramunida longior*	New Caledonia	BATHUS 2	CP 742	362-470	X	X	X		
S6	*Paramunida lophia*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		
S23	*Paramunida lophia*	Solomon Islands	SALOMON 2	CP 2199	135-325	X	X	X	X	X
S24	*Paramunida lophia*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		
PAR2	*Paramunida luminata*	Wallis and Futuna	MUSORSTOM 7	CP 616	550	X	X	X	X	X
PAR121	*Paramunida pictura*	Fiji	BORDAU 1	DW 1417	353	X	X	X		
PAR122	*Paramunida pictura*	Fiji	BORDAU 1	DW 1417	353	X	X	X	X	X
Fo177	*Paramunida pictura*	New Caledonia	NORFOLK 2	CP 1658	205-600	X	X	X	X	X
PAR4	*Paramunida polita*	Solomon Islands	SALOMON 2	CP 2260	399-427	X	X	X	X	X
PAR5	*Paramunida polita*	Solomon Islands	SALOMON 2	CP 2260	399-427	X	X	X		
PAR22	*Paramunida polita*	Indonesia	KARUBAR	CP 35	390-502	X	X	X	X	X
PAR23	*Paramunida polita*	Indonesia	KARUBAR	CP 35	390-502	X	X	X		
PAR65	*Paramunida polita*	Indonesia	KARUBAR	DW 25	336-446	X	X	X		
PAR66	*Paramunida polita*	Indonesia	KARUBAR	DW 25	336-446	X	X	X	X	X
PAR67	*Paramunida polita*	Indonesia	KARUBAR	CP 06	287-298	X	X	X		
PAR68	*Paramunida polita*	Indonesia	KARUBAR	CP 06	287-298	X	X	X		
PAR69	*Paramunida polita*	Indonesia	KARUBAR	CP 06	287-298	X	X	X		
PAR70	*Paramunida polita*	Indonesia	KARUBAR	CP 06	287-298	X	X	X		
PAR24	*Paramunida pronoe*	New Caledonia	NORFOLK 1	CP 1670	335-590	X	X	X	X	X
PAR25	*Paramunida pronoe*	New Caledonia	NORFOLK 1	CP 1670	335-590	X	X	X		
PAR18	*Paramunida proxima*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		
PAR61	*Paramunida proxima*	Vanuatu	MUSORSTOM 8	CP 1107	397-402	X	X	X		
PAR62	*Paramunida proxima*	Vanuatu	MUSORSTOM 8	CP 1107	397-402	X	X	X	X	X
S25	*Paramunida proxima*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X	X	X
S7	*Paramunida salai*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X	X	X
S29	*Paramunida salai*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		

PAR55	*Paramunida scabra*	Indonesia	KARUBAR	CP 86	223-225	X	X	X	X	X
PAR56	*Paramunida scabra*	Indonesia	KARUBAR	CP 86	223-225	X	X	X		
PAR57	*Paramunida scabra*	Indonesia	KARUBAR	CP 86	223-225	X	X	X		
PAR58	*Paramunida scabra*	Indonesia	KARUBAR	CP 86	223-225	X	X	X		
PAR90	*Paramunida scabra*	Indonesia	KARUBAR	CP 82	215-219	X	X	X		
PAR91	*Paramunida scabra*	Indonesia	KARUBAR	CP 82	215-219	X	X	X		
PAR31	*Paramunida setigera*	Philippines	MUSORSTOM 3	CP139	240-267	X	X	X	X	X
PAR32	*Paramunida setigera*	Philippines	MUSORSTOM 3	CP139	240-267	X	X	X		
PAR33	*Paramunida setigera*	Philippines	MUSORSTOM 3	CP139	240-267	X	X	X		
PAR34	*Paramunida setigera*	Philippines	MUSORSTOM 3	CP139	240-267	X	X	X		
PAR12	*Paramunida stichas*	New Caledonia	HALIPRO 1	CP 877	464-480	X	X	X		
PAR13	*Paramunida stichas*	New Caledonia	HALIPRO 1	CP 877	464-480	X	X	X		
PAR14	*Paramunida stichas*	New Caledonia	HALIPRO 1	CP 877	464-480	X	X	X		
PAR15	*Paramunida stichas*	New Caledonia	HALIPRO 1	CP 877	464-480	X	X	X	X	X
PAR19	*Paramunida stichas*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X	X	X
PAR35	*Paramunida stichas*	New Caledonia	MUSORSTOM 4	CP170	485	X	X	X		
PAR36	*Paramunida stichas*	New Caledonia	MUSORSTOM 4	CP170	485	X	X	X		
S27	*Paramunida stichas*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		
S28	*Paramunida stichas*	Solomon Islands	SALOMON 1	CP 1831	135-325	X	X	X		
Fo71	*Paramunida stichas*	New Caledonia	NORFOLK 1	CP 1684	210-590	X	X	X		
PAR10	*Paramunida thalie*	New Caledonia	LIFOU	DW 15	120-250	X	X	X	X	X
PAR135	*Paramunida thalie*	Tonga	BORDAU 2	DW 1583	327-360		X	X		
Fo28	*Paramunida thalie*	New Caledonia	NORFOLK 1	CP 1669	245-283	X	X	X		
Fo65	*Paramunida thalie*	New Caledonia	NORFOLK 1	CP 1683	245-283	X	X	X		
PAR78	*Paramunida tricarinata*	Philippines	MUSORSTOM 2	CP 35	160-198	X	X	X		
PAR79	*Paramunida tricarinata*	Philippines	MUSORSTOM 2	CP 35	160-198	X	X	X		
PAR80	*Paramunida tricarinata*	Philippines	MUSORSTOM 2	CP 35	160-198	X	X	X		
PAR155	*Paramunida tricarinata*	Taiwan	TAIWAN (NTOU)	CP 120	no depth record	X	X	X	X	X
PAR157	*Paramunida tricarinata*	Taiwan	TAIWAN (NTOU)	CP 120	no depth record	X	X	X		
PAR42	*Paramunida sp. 1*	New Caledonia	BATHUS 4	CP 946	386-430	X	X	X		
PAR43	*Paramunida sp. 1*	New Caledonia	BATHUS 4	CP 946	386-430	X	X	X		
PAR44	*Paramunida sp. 1*	New Caledonia	BATHUS 4	CP 946	386-430	X	X	X	X	X
PAR45	*Paramunida sp. 1*	New Caledonia	BATHUS 4	CP 946	386-430	X	X	X		
PAR107	*Paramunida sp. 1*	Fiji	MUSORSTOM 10	CP 1349	244-252	X	X	X		
PAR108	*Paramunida sp. 1*	Fiji	MUSORSTOM 10	CP 1349	244-252	X	X	X		
PAR109	*Paramunida sp. 1*	Fiji	MUSORSTOM 10	CP 1349	244-252	X	X	X	X	X
PAR110	*Paramunida sp. 1*	Fiji	MUSORSTOM 10	CP 1349	244-252	X	X	X		
PAR149	*Paramunida sp. 1*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X		
PAR150	*Paramunida sp. 1*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X	X	X
PAR151	*Paramunida sp. 1*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X		
PAR152	*Paramunida sp. 1*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X	X	X
PAR153	*Paramunida sp. 1*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X		
PAR148	*Paramunida sp. 2*	Vanuatu	BOA 0	CP 2327	287-440	X	X	X	X	X
PAR123	*Paramunida sp. 3*	Fiji	BORDAU 1	CP 1505	420-450	X	X	X	X*	X*
PAR139	*Paramunida sp. 4*	Vanuatu	SANTO	AT 34	234-270	X	X	X		
PAR140	*Paramunida sp. 4*	Vanuatu	SANTO	AT 34	234-270	X	X	X	X	X
PAR82	*Paramunida sp. 5*	Philippines	MUSORSTOM 2	CP 80	178-205	X	X	X	X	X
PAR83	*Paramunida sp. 5*	Philippines	MUSORSTOM 2	CP 80	178-205	X	X	X		
PAR84	*Paramunida sp. 5*	Philippines	MUSORSTOM 2	CP 80	178-205	X	X	X		
PAR85	*Paramunida sp. 5*	Philippines	MUSORSTOM 2	CP 80	178-205	X	X	X		
PAR100	*Paramunida sp. 5*	Philippines	MUSORSTOM 3	CP 90	195	X	X	X		
PAR101	*Paramunida sp. 5*	Philippines	MUSORSTOM 3	CP 90	195	X	X	X		
PAR102	*Paramunida sp. 5*	Philippines	MUSORSTOM 3	CP 90	195	X	X	X		
PAR103	*Paramunida sp. 5*	Philippines	MUSORSTOM 3	CP 90	195	X	X	X		
PAR17	*Paramunida sp. 6*	Tonga	BORDAU 2	CP 1643	487	X	X	X	X	X
Fo363	*Paramunida sp. 7*	French Polynesia	BENTHAUS	DW 1995	212-450	X	X	X		
Fo364	*Paramunida sp. 7*	French Polynesia	BENTHAUS	DW 1973	200-350	X	X	X	X	X
PAR97	*Paramunida sp. 8*	Chesterfield Islands	EBISCO	CP 2571	298-309	X	X	X	X	X
PAR98	*Paramunida sp. 8*	Chesterfield Islands	EBISCO	CP 2571	298-309	X	X	X		
Fo35	*Paramunida sp. 9*	New Caledonia	NORFOLK 1	CP 1670	400-440	X	X	X		
Fo185	*Paramunida sp. 9*	New Caledonia	NORFOLK 2	CP 1670	400-440	X	X	X	X	X
PAR75	*Paramunida sp. 10*	Madagascar	MD 08	CP 47	no depth record		X*			
PAR76	*Paramunida sp. 10*	Madagascar	MD 08	CP 47	no depth record		X*			
PAR77	*Paramunida sp. 10*	Madagascar	MD 08	CP 47	no depth record		X*			

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Locus	Primer	Direction	Sequence	Reference
COI	ParaCOIF	Forward	5'-GGM GCH TGR GCH GGH ATA G -3'	Cabezas et al (2009)
	ParaCOIF2	Forward	5'-ACA CTT TAY TTT ATY TTY GG -3'	This study
	ParaCOIR1	Reverse	5'-GGR TCT CCW CCW CCD GCR GGR TC -3'	Cabezas et al (2009)
ND1	ND1af-P	Forward	5?-CGG TTG ATC TTC AAA TTG TAA-3?	Pérez Barros et al (2008)
	ND1ar-P	Reverse	5?-AAG CTT ATC ATA TCG TAA ACG A-3?	Pérez Barros et al (2008)
	ND1ar	Reverse	5?-GGC AAA AAT CTT TTC CAG GCT AAG TA-3?	Zane et al (2000)
16S rDNA_1	Para16SF2	Forward	5?-CGR GYT TTT ATA TCT GGT T-3?	This study
	Para16SR	Reverse	5?-TTA TGC TAC CTT RGC ACA G-3?	This study
16S rDNA _2	Para16SF3	Forward	5?-AAA GGC CGC GGT ATA TTA A-3?	This study
	16Sbr-H	Reverse	5?-CCG GTC TGA ACT CAG ATC ACG T-3?	Palumbi (1991)
18S rDNA_1	18S 1f	Forward	5?-TAC CTG GTT GAT CCT GCC AGT AG-3?	Whiting (2002)
	18S b2.9	Reverse	5?-TAT CTG ATC GCC TTC GAA CCT CT-3?	Whiting (2002)
18S rDNA _2	18S 5FrRNA	Forward	5?-GCG AAA GCA TTT GCC AAG AA-3?	Carranza *et al* (1996)
	18S 9RrRNA	Reverse	5?-GAT CCT TCC GCA GGT TCA CCT AC-3?	Carranza *et al* (1996)
28S rDNA_1	28SAF	Forward	5?-AGT AAG GGC GAC TGA AMM GGG A-3?	Palero *et al* (2008)
	28SAF-Par	Forward	5´-GGA KGA GCC CAG CGC ATA A-3´	This study
	28SAR	Reverse	5?-CAC ATG TTG GAC TCC TTG GCC CG-3?	Palero *et al* (2008)
28S rDNA _2	28SAR-Par	Reverse	5?-CTC AAT CAC CTT BAT TRC GCC-3?	This study
	28SBF	Forward	5?-CGG GCC AAG GAG TCC AAC ATG TG-3?	Palero *et al* (2008)
	28SBR	Reverse	5?-CCC ACA GCG CCA GTT CTG CTT ACC-3?	Palero *et al* (2008)

Table 2. Loci and primers used in this study to amplify and sequence mitochondrial and nuclear genes.

	a	**b**	**c**	**d**	**e**	**f**	**g**
a	1	0.3	0.7	0.01	0.6	0.3	0.5
b	0.3	1	0.5	0.01	0.7	0.8	0.8
c	0.7	0.5	1	0.01	0.6	0.5	0.7
d	0.01	0.01	0.01	1	0.01	0.01	0.01
e	0.6	0.7	0.6	0.01	1	0.8	0.8
f	0.3	0.8	0.5	0.01	0.8	1	0.7
g	0.5	0.8	0.7	0.01	0.8	0.7	1

Table 3. Dispersal rates between areas. See text for correspondence between letter code and areas.

Gene fragment	COI	ND1	16S rRNA	Mitochondrial	18S rRNA	28S rRNA	Nuclear	Combined
Type	mtDNA	mtDNA	mtDNA	mtDNA	nDNA	nDNA	nDNA	Both
Total sites	575	460	912	1947	1797	1783	3580	5527
Informative sites	204 (35%)	188 (40%)	364 (39%)	756 (38%)	109 (6%)	330(18%)	439 (12%)	1119 (20%)
Model	GTR+I+G	TrN+I+G	K81uf+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G
Base frequency								
%A	31.14	31.28	40.70	36.89	25.75	26.39	25.93	29.05
%C	15.78	4.6	5.05	8.54	21.50	18.49	20.04	15.85
%G	14.82	17.15	15.19	14.37	24.94	27.05	26.19	22.63
%T	38.26	46.92	39.06	40.20	27.81	28.08	27.85	32.47
Rate matrix								
[A-C]	4.1043	1	1	1.1528	0.7845	0.8935	0.8459	0.8224
[A-G]	13.1039	12.4884	10.3472	10.7793	2.9843	1.9433	2.0997	5.4762
[A-T]	7.2933	1	2.7137	2.3502	1.8082	1.0216	1.1403	2.6046
[C-G]	0.4854	1	2.7137	0.7311	0.4530	0.2988	0.3191	0.4402
[C-T]	38.5872	19.7347	10.3472	13.5511	4.2811	3.8318	3.6251	6.5925
[G-T]	1	1	1	1	1	1	1	1
Shape parameter	0.9757	0.6502	1.021	0.8999	0.9837	0.6490	0.7013	0.5286
Invariable sites	0.5774	0.5019	0.4458	0.5126	0.7801	0.4855	0.6497	0.5931

Table 4. Mitochondrial, nuclear and combined datasets including informative sites and maximum likelihood models selected through AIC criterion as implemented in ModelTest. Base frequencies, rate matrix, gamma shape parameter and proportion of invariable sites are showed.

COI		**ND1**		**16S rRNA**		**18S rRNA**		**28S rRNA**	
Intraspecific (%)									
Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
0.43	0-1.39	0.53	0-1.53	0.19	0-0.95	0.05	0-0.23	0.10	0-0.49
Interspecific (%)									
Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
12.10	1.56-18.61	12.47	2.17-21.06	9.26	2.86-18.17	1.50	0-5.47	3.91	0.24-7.86

Table 5. Average intra and interspecific divergence among *Paramunida* species.

Discusión

En esta Tesis Doctoral se ha abordado el estudio de la taxonomía y filogenia de distintos géneros de la familia Galatheidae Samouelle, 1819, desde una aproximación al estudio de caracteres morfológicos y moleculares. De esta manera, y en combinación con otros análisis, el objetivo ha sido proporcionar un marco taxonómico, filogenético y biogeográfico robusto para poder interpretar la historia evolutiva de la familia. Los resultados aquí presentados muestran como la incorporación de herramientas moleculares al estudio de los caracteres morfológicos resulta extremadamente útil tanto para estimar el valor taxonómico de estos últimos, así como para inferir diferentes aspectos como el origen y modo de diversificación del grupo.

Evaluación de la variabilidad morfológica

Como ya ha sido destacado en los diferentes capítulos de la presente Tesis, los galateidos representan una fauna muy conspicua de los hábitats bentónicos, estando distribuidos desde aguas superficiales hasta profundidades superiores a los 5.000 metros (Baba, 2005). Históricamente, el grupo ha recibido una gran atención taxonómica (A. Milne Edwards, 1880; Bonnier, 1888; Henderson, 1888, Faxon, 1895; A. Milne Edwards y Bouvier, 1900; Benedict, 1902; Chace, 1942), pero fue a partir de la década de los años 60 cuando comenzó un aumento exponencial de la descripción tanto de nuevos géneros como especies (Baba *et al.*, 2008). De hecho, aproximadamente la mitad de la diversidad actual conocida ha sido descrita desde comienzos de los años 80, con una notable contribución tras las revisiones del material procedente de las campañas históricas *Albatross* (1907-1910) y *Galathea* (1950-1052) (Baba, 1988; 2005).

Como se ha indicado anteriormente, la familia Galatheidae es un grupo en continuo cambio, describiéndose cada año nuevos géneros y especies, lo que sugiere que aún estamos lejos de conocer la diversidad real del grupo. De hecho, durante el desarrollo de este trabajo se han descubierto un género y 22 especies nuevas para la Ciencia, destacándose el valor taxonómico de sutiles diferencias morfológicas asociadas con el caparazón, esternitos torácicos, antena, anténula, tercer maxilípedo

(Mxp 3), quelípedos (P1) y pereiópodos (P2-P4) tanto a nivel intergenérico como a nivel interespecífico.

Nivel intergenérico

En el caso del género *Babamunida*, los caracteres morfológicos que resultaron útiles para diferenciarlo de otros géneros estrechamente relacionados como *Munida* Leach, 1820 fueron muy sutiles, y se tuvieron que emplear técnicas de microscopía electrónica de barrido para evaluar el grado de variabilidad morfológica de caracteres asociados con la región epistómica. Esta estructura no había sido previamente analizada en la familia Galatheidae, a pesar de que trabajos previos ya habían demostrado su utilidad en otras grupos de decápodos como Varunidae (Ng *et al.*, 1999), Cambaridae (Cooper, 2006) y Glypheoidea (Schram y Ahyong, 2002). Igualmente sucede con el estudio de caracteres larvarios, los cuáles han sido ampliamente utilizados en estudios taxonómicos con otros decápodos (Schubart *et al.*, 2002; Hultgren y Stachowicz, 2008), pero su utilidad no había sido previamente testada en galateidos.

Los resultados obtenidos en el Capítulo I sugieren que tanto el estudio morfológico de la primera larva zoea, así como de la región epistómica representan una fuente adicional de caracteres taxonómicos a nivel de género. El estudio de caracteres larvarios está muy limitado debido a la dificultad para obtener hembras ovígeras; sin embargo, el análisis de la región epistómica es fácil de abordar y por tanto sería recomendable que futuros estudios taxonómicos lo incorporaran de manera rutinaria.

Nivel interespecífico

A nivel interespecífico, el estudio morfológico de los géneros de aguas profundas *Munida* Leach, 1820, *Agononida* Baba y de Saint Laurent, 1996, *Plesionida* Baba y de Saint Laurent, 1996 y *Paramunida* Baba, 1988 reveló la existencia de nuevos taxones sólo distinguibles por ligeras variaciones en la morfología de caracteres asociados con el caparazón, los segmentos antenales y antenulares y los pereiópodos.

El género *Munida* representa el grupo más diverso dentro de la familia Galatheidae (Baba *et al*., 2008), siendo su estudio taxonómico muy complejo debido a que los caracteres morfológicos presentan una gran similitud (Machordom y Macpherson, 2004; Baba, 2005). En la presenta Tesis no se llevó a cabo la revisión completa del género, pero nuestros resultados constataron el valor taxonómico de diferencias morfológicas presentes en los pereiópodos y los segmentos antenales y antenulares. La heterogeneidad encontrada en las divergencias genéticas a nivel interespecífico, así como la falta de apoyo a la monofilia del grupo sugiere la existencia de nuevos linajes dentro del género y la necesidad de una profundad revisión. Igualmente, un estudio más detallado debería llevarse a cabo en el género *Agononida*, con el objetivo de clarificar los caracteres apomórficos que definen el grupo, así como la posición taxonómica de algunas de sus especies. Por último, la descripción de la especie *Plesionida concava* n.sp. incrementó el número de especies conocidas para el género a tres, destacando la importancia en dicho género de caracteres como la espinulación del caparazón y los quelípedos, así como como la forma de los pereiópodos.

Dentro del género *Paramunida*, las ligeras diferencias tanto en forma y longitud de los segmentos y espinas antenales y antenulares fueron fundamentales para poder determinar el estatus taxonómico de las nuevas especies y diferenciarlas de las especies nominales donde algunas de ellas habían sido previamente adscritas. En el caso de la especie *P. granulata* (Henderson, 1885), tanto su posición basal dentro del género así como una marcada diferencia morfológica en el tamaño de la espina distomesial del segundo segmento antenal, sugieren que podría ser el único representante de un nuevo género. Por otro lado, caracteres como la estriación y la distribución de las sedas a lo largo del surco cervical, resultaron de gran utilidad para diferenciar las distintas especies. Respecto al tipo de estría se pudieron distinguir tres grandes grupos en base a la presencia de diminutos gránulos, estrías largas con filas de espinas o estrías cortas con una o pocas espinas en la base. Por otro lado, la presencia y distribución de las sedas en el caparazón fue de extrema utilidad para diferenciar especies muy próximas como *P. scabra* (Henderson, 1885) y *P. crinita* n.sp. Otros caracteres estudiados como la espinulación de las regiones mesogástrica y cardíaca han sido ampliamente utilizados en galateidos (p.e. género *Plesionida*) pero no

así el tipo de estría del caparazón y la distribución de las sedas, siendo interesante una futura reexaminación de estos caracteres en otros géneros de la familia.

La revisión del género *Allogalathea* Baba, 1969 demostró la existencia de nuevos linajes y la importancia de caracteres asociados con la forma y longitud de rostro así como la longitud, espinulación y distribución de las sedas en los pereiópodos. Hasta la revisión llevada a cabo en el presente trabajo, el género estaba considerado como monoespecífico e incluía únicamente la especie *Allogalathea elegans* (Adams y White, 1848). Trabajos previos ya habían destacado la presencia de distintos patrones de color, así como un distinto número de epipodios en los pereiópodos y pequeñas variaciones morfológicas en los quelípedos y forma del rostro (Miyake, 1938; Baba, 1979). Nuestros resultados constataron el valor taxonómico de esas sutiles diferencias asociadas al quelípedo y al rostro, siendo la proporción relativa de las patas marchadoras otro carácter útil para distinguir especies. Por otro lado, tanto el número de epipodios como su presencia/ausencia en los pereiópodos no parecen ser caracteres taxonómicamente válidos para delimitar especies en el género *Allogalathea*, puesto que presentan una gran variabilidad a nivel intraespecífico. Este último carácter ha sido ampliamente utilizado para describir especies en otros géneros de aguas superficiales como *Galathea* (Osawa, 2004; Baba, 2005), por lo tanto sería recomendable una reevaluación de ese material con el objetivo de constatar el estatus taxonómico de la especies descritas en base a dichas diferencias morfológicas.

Respecto a los patrones de coloración, solamente la especie *A. babai* presenta una única banda central de color claro en el caparazón, lo que permite su inequívoca identificación y delimitación dentro del género. Para el resto de especies no pudo identificarse un único patrón característico, presentando una gran variabilidad intraespecífica el color del caparazón, y habiéndose observado la existencia de mimetismo críptico en las distintas especies de *Allogalathea* y los crinoideos a los que se asocian (Fujita, Y. comunicación personal). En otras familias de decápodos como Diogenidae o Palinuridae, los patrones de coloración son suficiente evidencia para delimitar especies (Ravago y Juinio-Meñez, 2002; Poupin y Malay, 2009). La familia Galatheidae se caracteriza por poseer coloraciones muy llamativas (Baba *et al.*, 2008),

y aunque en algunos géneros como *Raymunida* Macpherson y Machordom, 2000 parece mostrar cierta utilidad para diferenciar especies (Macpherson y Machordom, 2001), no es un carácter habitualmente estudiado puesto que gran parte del material pierde su color original tras la conservación. El fenómeno de mimetismo críptico ha sido previamente observado en otros crustáceos de la familia Palaemonidae (Marin y Chan, 2006), por lo que este hecho plantea interesantes cuestiones acerca de la existencia de patrones comunes en diferentes grupos de crustáceos.

Los resultados aquí presentados muestran la gran variedad de caracteres diagnósticos empleados para ordenar la diversidad biológica dentro la familia Galatheidae, así como el valor taxonómico de sutiles diferencias morfológicas. Futuras investigaciones incluyendo un mayor número de taxones así como un mayor número de datos morfológicos (adultos y larvarios), nos permitirán mejorar el conocimiento de la evolución de los caracteres morfológicos así como identificar las sinapomorfías que definen cada uno de los géneros de la familia.

Evaluación de la variabilidad molecular

La mayor parte de trabajos de alfa taxonomía continúan supeditados al complejo estudio de los caracteres morfológicos, siendo un método no neutral y que en muchos casos conlleva a la infraestimación de la biodiversidad real (Lefébure *et al.,* 2006). En ese sentido, el campo de la sistemática ha sufrido una gran revolución desde la incorporación de técnicas moleculares como la reacción en cadena de la polimerasa (PCR) (Tautz *et al*., 2003), que permite amplificar regiones específicas del ADN a partir de pequeñas cantidades de material biológico. De este modo, en los últimos años ha surgido un creciente interés por el estudio de distintos marcadores moleculares que permitan resolver tanto problemas taxonómicos como relaciones filogenéticas (Hajibabaei *et al*., 2007).

Con anterioridad, el número de trabajos que incorporaban caracteres moleculares a estudios taxonómicos en la familia Galatheidae eran muy escasos y todos ellos se limitaban al empleo de marcadores mitocondriales (Macpherson y Machordom, 2001; Lin *et al.,* 2004; Machordom y Macpherson, 2004). Teniendo en cuenta dicha consideración, el presente estudio abordó el análisis taxonómico y

filogenético de varios géneros de la familia Galatheidae, empleando caracteres morfológicos en combinación con marcadores moleculares tanto de origen mitocondrial como nuclear.

Detección de divergencias genéticas

Como ya se destacó en la Introducción, son muchas las definiciones que se han propuesto para el término especie, no existiendo unos límites estandarizados que permitan su clara delimitación. La inclusión de marcadores moleculares a estudios taxonómicos añade una fuente de información adicional, y permite detectar diferencias que en muchos casos pasan desapercibidas al ojo humano. Aunque algunos trabajos han intentado establecer un valor de divergencia genética que permita decidir cuándo dos taxones pertenecen a entidades taxonómicas diferentes (Hebert *et al.,* 2004; Lebéfure *et al.,* 2006), el grado de correlación entre la divergencia morfológica y molecular no está claro, siendo elección del taxónomo la propuesta de nuevos linajes.

Para la identificación de los nuevos taxones aquí descritos se analizó un número similar de genes al de otros trabajos previos que han estudiado la sistemática tanto de la familia Galatheidae (Lin *et al*., 2004; Machordom y Macpherson, 2004) como de grupos próximos (Pérez-Losada *et al*., 2004; Malay y Paulay, 2009). Siempre que fue posible se analizó más de un ejemplar por especie tanto a nivel morfológico como molecular con el objetivo de estudiar la variabilidad intraespecífica; sin embargo, en algunos casos los análisis moleculares sólo pudieron llevarse a cabo con éxito en un único espécimen.

En primer lugar se abordó el estudio de una serie de ejemplares previamente clasificados dentro del género *Munida*. En un trabajo previo en el que se analizaban las relaciones filogenéticas del género *Munida* y afines, se puso de manifiesto la clara divergencia genética existente entre la especie *Munida callista* Macpherson, 1994 y el resto de especies del género. De hecho, esos valores eran incluso mayores que los existentes entre el género *Munida* y otras especies pertenecientes a géneros distintos (p.e. *Paramunida* y *Raymunida*), por lo que se sugería la posible adscripción a un género diferente de la especie *M. callista*.

De esta manera se estudiaron morfológica y molecularmente ésta y otras especies estrechamente relacionadas con el objetivo de confirmar su estatus taxonómico. Los análisis llevados a cabo permitieron constatar la existencia de un nuevo género dentro de la familia Galatheidae, y tanto el gen mitocondrial COI como el ARNr 16S apoyoran claramente su existencia. Los valores de divergencia intragenéricos estuvieron dentro del rango 5.2-11.09% para el ARNr 16S y entre un 15.37-15.52% para el COI. Dichos valores aunque bastante elevados, se encuentran dentro del rango observado para otros géneros de la familia como *Bathymunida* (Balss, 1914) o *Munidopsis* Whiteaves, 1784 (Machordom y Macpherson, 2004; Jones y Macpherson, 2008), y son similares a los encontrados en otros decápodos como langostas (Ptacek *et al.,* 2001) o cangrejos braquiuros (Harrison, 2004; Costa, 2007). Así, el estudio de los caracteres morfológicos en combinación con los marcadores moleculares apoyaron la existencia del género *Babamunida*, y la inclusión de las especies *Munida callista*, *Munida plexaura*, *Munida hystrix*, *Munida brucei* y *Munida javieri* como parte del mismo.

A lo largo de los restantes capítulos de esta Tesis se analizó la variabilidad genética de marcadores tanto de origen mitocondrial como nuclear, con el objetivo de constatar la existencia de divergencia genética en las 22 nuevas especies descritas. Concretamente en el capítulo II se analizaron especímenes pertenecientes a los géneros *Agononida*, *Paramunida, Plesionida* y *Munida.* Dentro de los géneros *Agononida* y *Munida*, las divergencias medias observadas fueron elevadas (10% y 15% respectivamente), lo que podría guardar relación con problemas de saturación de los marcadores empleados. Sin embargo, en todos los casos los niveles de divergencia genética fueron mayores a medida que aumentaba la distancia evolutiva entre los taxones analizados, lo que sugiere que los marcadores empleados no estaban saturados. Este hecho sugiere que algunas especies adscritas a los géneros *Agononida* o *Munida* podrían pertenecer a entidades taxonómicas diferentes, por lo que como ya se ha destacado previamente, requieren de una revisión sistemática más profunda.

Para el estudio del género *Paramunida* se seleccionó un gen mitocondrial adicional (ND1), el cuál mostró niveles de variabilidad similares al COI, lo que sugiere que podría ser un buen candidato para trabajar a niveles taxonómicos bajos

como género y especie. Los valores de divergencia genética observados para los genes mitocondriales mostraron un rango entre 1.56-21.06%. En todos los genes analizados (ND1, ARNr 16S y COI), los mayores valores de divergencia fueron observados con respecto a la especie *P. granulata*. Tanto los elevados valores de divergencia con respecto al resto de especies adscritas al grupo así como la presencia de una conspicua diferencia morfológica asociada a la espina distomesial del segundo segmento antenal sugieren su posible pertenencia a nuevo género. Sin embargo, en el presente trabajo se decidió no modificar su estatus taxonómico a la espera de encontrar otros linajes que muestren caracteres morfológicos similares. Respecto a los genes nucleares, el valor de divergencia media para las distintas especies del género *Paramunida* fue de un 2.8% para el ARNr 18S y de un 3.8% para el ARNr 28S. Estos valores son similares a los que se han encontrado en otros grupos de decápodos como Achelata, Thalassinidea o Brachyura (Toon *et al.,* 2009). El gen ARNr 18S mostró una menor variabilidad y en algunos casos no permitió diferenciar genéticamente especies del género *Paramunida*, por lo que se puede concluir que el marcador ARNr 28S es de mayor utilidad para detectar divergencias genéticas dentro de la familia Galatheidae. El estudio de marcadores moleculares para la revisión taxonómica del género *Paramunida* fue determinante, puesto que permitió detectar divergencias genéticas entre especímenes que habían sido clasificados bajo el mismo taxón nominal durante el análisis morfológico previo.

Por otro lado, para la revisión del género *Allogalathea* se estudiaron los marcadores mitocondriales ARNr 16S y COI en combinación con el gen nuclear PEPCK. Al igual que en anteriores capítulos, los genes ARNr 16S y COI fueron útiles para diferenciar las distintas especies del género y permitieron diferenciar claramente cuatro clados (*A. elegans*, *A. babai* n.sp., *A. inermis* n.sp. and *A. longimana* n.sp.). Las divergencias intraespecíficas no mostraron solapamiento con los valores de divergencia entre especies, aunque uno de los ejemplares pertenecientes a la especie *A. babai* n.sp. mostró una divergencia media intraespecífica para ambos genes mitocondriales de un 4.5%. Como se ha mostrado a lo largo de este y otros trabajos (Macpherson y Machordom, 2001, Lin *et al.,* 2004) dichos valores junto con diferencias morfológicas son suficiente evidencia para poder definir la existencia de una nueva especie; sin embargo, un estudio morfológico detallado de dicho ejemplar

no permitió la identificación de ninguna autapomorfía, por lo que se considera como parte de la especie *A. babai* n.sp.

A nivel nuclear se decidió estudiar el gen PEPCK puesto que trabajos recientes sugerían su posible utilidad para estudiar la sistemática de decápodos en niveles taxonómicos bajos como género y especie (Tsang *et al.*, 2008; Ma, Chan y Chu, 2009). Dentro del género *Allogalathea* se observó una divergencia genética entre 0.5 y 3.5%, pero no fue lo suficientemente informativo como para delimitar los taxones *A. elegans* y *A. longimana* n.sp., por lo que dicho marcador no parece recomendable para estudiar la variación genética a nivel intragenérico dentro de la familia Galatheidae.

Los valores de divergencia observados entre las distintas especies aquí estudiadas mostraron un rango entre un 1-14% para el gen ARNr 16S, entre un 3-21% para el COI y entre un 2-21% para el ND1. Esta gran heterogeneidad hace imposible establecer un valor de divergencia de medio para delimitar especies dentro de la familia. Además, en los diferentes capítulos se observaron especies que morfológicamente eran muy próximas y genéticamente mostraban los valores de divergencia más bajos (p.e *A. similis* y *A. isabelensis* n.sp.), en contraste con especies que mostraron valores de divergencia muy elevados asociados con sútiles diferencias morfológicas (p.e. *Allogalathea*). Estos resultados apoyan la falta de correlación entre divergencia genética y morfológica, y destacan la gran utilidad de los marcadores moleculares para confirmar el valor taxonómico de diferencias morfológicas.

Análisis de las relaciones filogenéticas

La reconstrucción de las relaciones evolutivas en decápodos ha tomado dos claras direcciones en los últimos años: 1) el empleo de marcadores moleculares que codifican para proteínas y que pueden proporcionar una mayor resolución para resolver las relaciones basales (Tsang *et al.,* 2008; Ma *et al.,* 2009) o 2) la incorporación de la mayor cantidad de marcadores posibles (ribososomales y codificantes) (Porter *et al.,* 2005; Bracken *et al.,* 2009). Desde nuestro punto de vista, la segunda estrategia parece ser más útil, puesto que la combinación de múltiples genes con distintas tasas

de mutación proporciona una mayor información a distintas escalas temporales, así como un mejor apoyo estadístico.

En primer lugar se analizaron las relaciones evolutivas del género *Babamunida* a nivel intraespecífico e intergenérico empleando los marcadores moleculares ARNr 16S y COI. Los distintos análisis filogenéticos apoyaron claramente la monofilia del género descrito (NJ, MP, ML e IB). Se diferenciaron dos clados, uno incluyendo las especies *B. hystrix* y *B. javieri* y otro *B. plexaura* y *B. callista*; sin embargo, la relación evolutiva entre estas dos últimas especies no fue soportada. Asimismo, no pudo establecerse con un apoyo estadístico alto la posición filogenética del nuevo género dentro de la familia, y solo el análisis bayesiano y de parsimonia soportaron su relación de grupo hermano con el género *Crosnierita* (Macpherson, 1998). Esta falta de resolución podría deberse a problemas de saturación en los marcadores mitocondriales seleccionados (homoplasia); sin embargo, el número de posiciones informativas de cada uno de ellos sugería que ambos eran idóneos para este tipo de estudio. Otra causa podría estar relacionada con el hecho de que la diversidad real del género *Babamunida* fuera mayor de lo que actualmente conocemos; de hecho, hay un nuevo linaje en fase de descripción (K. Baba, com. pers.) y recientemente se ha descrito la especie *Babamunida kanaloa* de las islas Hawaii (Schnabel *et al.*, 2009). En este último trabajo, un análisis de parsimonia con los mismos marcadores apoyó la existencia de un clado incluyendo las especies *B. kanaloa*, *B. hystrix* y *B.javieri* y otro incluyendo la especie *B. plexaura*. Estos resultados concuerdan con los aquí mostrados, mostrando las especies incluidas en el primer grupo una mayor similitud morfológica en el quelípedo y el caparazón. Posiblemente, el descubrimiento de nuevos taxones ayudará a inferir con mayor robustez las relaciones entre las distintas especies, así como la posición filogenética de las especies *B. callista* y *B. plexaura*.

A modo de conclusión para el Capítulo I cabe destacar la utilidad de los marcadores mitocondriales ARNr 16S y COI, en tanto que representan una fuente de información adicional en estudios taxonómicos basados en caracteres morfológicos. Sin embargo, no resultan útiles para realizar inferencias filogenéticas robustas dentro de la familia Galatheidae, por lo que su empleo es más recomendable en combinación con marcadores adicionales.

Por otro lado, los resultados obtenidos en el estudio de las relaciones filogenéticas de varios géneros de la familia (Capítulo II, III y V), mostraron un patrón similar de falta de resolución en los nodos basales de las reconstrucciones filogenéticas, la cual se mantenía incluso cuando la información de distintos marcadores era analizada de manera conjunta. Respecto a la conveniencia de analizar conjuntamente genes mitocondriales y nucleares para inferir relaciones filogenéticas ha habido mucho debate (Huelsenbeck *et al.*, 1996). De manera general, parece que el análisis combinado de marcadores que muestren una misma señal proporciona reconstrucciones filogenéticas más precisas y robustas, en tanto que se aumenta el número de caracteres informativos y se combinan marcadores con distintos poderes resolutivos (Phillips *et al.*, 2006; Sharon *et al.*, 2006). Sin embargo, dichos marcadores no siempre muestran el mismo tipo de historia evolutiva, pudiendo mostrar propuestas filogenéticas discordantes debido al efecto de la hibridación o barridos selectivos (Sota y Vogler, 2001; Shaw, 2002; Gompert *et al.*, 2008).

En el capítulo II se decidió combinar la información de ambos marcadores mitocondriales puesto que ambos mostraban una misma propuesta filogenética. En el caso del género *Agononida* ninguno de los análisis llevados a cabo apoyó la monofilia del grupo y tampoco pudieron resolverse las relaciones evolutivas ente las distintas especies con un alto apoyo estadístico. Trabajos previos tampoco han podido identificar un origen común para el género (Machordom y Macpherson, 2004), por lo que como ya se ha destacado anteriormente es necesario hacer una revisión profunda del género con el objetivo de clarificar su sistemática. Por otro lado, el género *Plesionida* fue propuesto en base a caracteres morfológicos (Baba y de Saint Laurent, 1996), habiendo confirmado nuestros resultados su estatus taxonómico así como su relación de grupo hermano con el género *Paramunida*.

El estudio del género *Paramunida* se abordó en distintos capítulos de esta Tesis. En primer lugar se describieron dos nuevos taxones para la región de las Islas Salomón y se llevó a cabo una reconstrucción parcial de las relaciones filogenéticas del grupo. En esta primera aproximación se destacó la posición basal de la especie *P. granulata*, la existencia de estructura genética entre distintas poblaciones de la especies *P. stichas* así como una falta de resolución en los nodos más basales de la filogenia.

Puesto que el empleo de marcadores nucleares ha mostrado gran utilidad para resolver las relaciones filogenéticas entre distintos géneros de decápodos (Pérez-Losada *et al.,* 2004; Palero *et al.,* 2009), se recurrió a su estudio con el objetivo de testar si dicha falta de resolución era debida a un artefacto generado por los marcadores empleados hasta la fecha, o por el contrario guardaba relación con la historia evolutiva del grupo.

Nuestros análisis apoyaron la existencia de once nuevas especies en adición a las 26 especies previamente descritas para el grupo (Baba *et al.,* 2008), lo que representaba un incremento del 38% sobre su diversidad. Resultados similares han sido observados en otros taxones marinos, donde el número de morfoespecies descritas tiende a ser una infraestimación de la biodiversidad real del grupo (Knowlton, 1986; Meyer 2003; Malay y Paulay 2009). Asimismo se detectó estructura poblacional entre las regiones de Nueva Caledonia, Vanuatu, Islas Salomón y Fiji, lo que sugiere la existencia de alguna barrera al flujo génico así como un incipiente proceso de especiación. Por otro lado, el análisis independiente de los genes mitocondriales no apoyó la monofilia del género puesto que la relación de la especie *P. granulata* con el resto de representantes del mismo no fue altamente soportada. Sin embargo, tanto el análisis de los genes nucleares como el análisis combinado de marcadores mitocondriales y nucleares sí apoyó su estatus taxonómico, por lo que como ya se ha destacado se tomó la decisión de no modificar su entidad taxonómica. Las relaciones filogenéticas entre las distintas especies fueron resueltas con un mayor soporte en los nodos terminales, y aunque la inclusión de marcadores nucleares permitió mejorar la resolución en algunos nodos internos, se mantuvo la falta de resolución.

Este patrón se mantuvo para el género *Munida*, y aunque todos los análisis apoyaron claramente la existencia de cuatro nuevas especies, no pudieron resolverse sus relaciones evolutivas con el resto de linajes. Cabe destacar la existencia de dos clados claramente diferenciados a nivel genético y aunque un análisis preliminar no permitió la identificación de sinapomorfías, es necesario analizar los caracteres morfológicos asociados con la región del epistoma, ya que como se ha mostrado aquí muestran gran utilidad para identificar nuevos taxones dentro del género *Munida*.

Dentro de uno de estos clados se incluía la especie *M. rugosa* (Fabricius, 1775), especie tipo del grupo y que presenta distribución Atlántico-Mediterránea. En este clado, además se incluían otras cuatro especies del género con distribución Indo-Pacífica; sin embargo, las relaciones filogenéticas entre las distintas especies no pudieron ser resueltas con apoyo estadístico y la especie *M. rugosa* siempre aparecía en posición basal. Este resultado enfatiza la necesidad de realizar una profunda revisión incluyendo un mayor número de especies de la región Atlántico-Mediterránea con el objetivo de determinar el estatus taxonómico del género en las diferentes cuencas oceánicas.

Por último, se estudiaron las relaciones filogenéticas entre las diferentes especies descritas para el género *Allogalathea*. Al igual que en anteriores capítulos, los genes mitocondriales apoyaron la monofilia del grupo así como el estatus de los taxones descritos; sin embargo, las relaciones entre las diferentes especies no pudieron ser resueltas. La inclusión de un gen nuclear más conservado tampoco permitió resolver la sistemática del género, lo que sugiere que dicho marcador no es útil para analizar las relaciones evolutivas a nivel de género dentro de la familia Galatheidae. Sin embargo, datos preliminares no mostrados en la presente Tesis sugieren un mayor poder discriminante para aclarar las relaciones evolutivas a nivel de familia.

Esta falta de apoyo estadístico para establecer las relaciones dentro y entre diferentes géneros de la familia en los nodos internos, ya fue destacada en un trabajo previo donde se analizaron las relaciones filogenéticas de *Munida* y géneros afines (Machordom y Macpherson, 2004). Tanto ese trabajo como nuestros resultados (número de caracteres informativos y ausencia o baja saturación de los marcadores), sugieren que tal hecho debe estar más relacionado con la historia evolutiva del grupo que con los marcadores genéticos seleccionados. La existencia de un evento de rápida diversificación acontecido durante el Mioceno se ha propuesto como la hipótesis más plausible para explicar esa falta de resolución; sin embargo, dicha hipótesis no había sido estadísticamente testada hasta la fecha. De esta manera se exploró el modo y el tiempo de diversificación de la familia Galatheidae tomando como modelo el género *Paramunida*.

Historia evolutiva de la familia Galatheidae

La familia Galatheidae con 34 géneros descritos hasta la fecha, es una de las más diversas dentro del infraorden Anomura (McLaughlin *et al.*, 2007), y aunque en términos taxonómicos ha recibido una gran atención, son muy pocos los trabajos que han abordado aspectos de índole más ecológica, biológica o evolutiva (p.e. Gómez-Gutiérrez y Sánchez-Ortíz, 1997; Machordom y Macpherson, 2004; Fujita y Shokita, 2005). Actualmente, y tras el esfuerzo llevado a cabo principalmente por países como Francia y Australia en aguas del Pacífico, se tiene un muestreo razonablemente exhaustivo para un gran número de taxones de la familia (http://www.mnhn.fr/musorstom). De esta manera, en este trabajo hemos podido interpretar la historia evolutiva de la familia Galatheidae desde una perspectiva morfológica y molecular, tomando como modelo el género *Paramunida* y estableciendo una escala espacio-temporal para el origen y diversificación del grupo.

Estasis morfológica

Una proporción significativa de los trabajos filogenéticos más recientes basados en crustáceos se ha centrado en el orden Decapoda, un taxón cuya diversidad actual está estimada en aproximadamente unas 15.000 especies (Ahyong *et al.*, 2007; Chu *et al.*, 2009). Dentro de ese grupo, un gran número de géneros han sido descritos para la familia Galatheidae (Baba *et al.,* 2008), principalmente para acomodar especies que inicialmente habían sido descritas para el género *Munida* (Baba y de Saint Laurent, 1996; Macpherson y Machordom, 2000).

Este hecho ha estado claramente influenciado por la extrema similitud morfológica existente entre los diferentes géneros de la familia, lo que dificulta la identificación de caracteres diagnósticos (Jones y Macpherson, 2007). Fenómenos de convergencia o estasis en la evolución de los caracteres morfológicos parecen ser comunes en decápodos, incluso entre linajes evolutivos muy divergentes a nivel genético (Knowlton, 1986; Schubart *et al.*, 2000a). Se ha argumentado que condiciones ambientales muy extremas pueden derivar en una selección estabilizadora sobre los caracteres morfológicos, reduciendo e incluso eliminando el cambio morfológico que puede acompañar el proceso de especiación (Bickford *et al.*, 2007). Trabajos previos han sugerido que los fenómenos de especiación críptica

podrían ser aparentemente más comunes en el medio marino, debido a la dificultad para evaluar pautas de comportamiento y porque los organismos acuáticos a menudo emplean señales químicas para el reconocimiento de gametos (Stanhope *et al.*, 1992; Knowlton, 2000).

En el caso de la familia Galatheidae, la falta de conocimiento acerca de muchos aspectos de su biología, hábitat y comportamiento hacen difícil evaluar qué factores pueden estar determinando tanto la gran similitud morfológica como la existencia de especies morfológicamente muy próximas y genéticamente muy distantes. Aproximadamente el 85% de los géneros de la familia están asociados a aguas profundas, por lo que podría hipotetizarse que la mayor estabilidad y homogeneidad del medio a esas profundidades hubiera causado una presión selectiva sobre esos morfotipos. Sin embargo, nuestros resultados también han mostrado la existencia de especies crípticas dentro del género *Allogalathea*, el cuál se encuentra principalmente distribuido en aguas someras. Por lo tanto, parece más probable que factores intrínsecos relacionados con los mecanismos de especiación del grupo sean más determinantes que las condiciones ambientales. Con la información de que disponemos actualmente no es posible determinar si las similitudes fenotípicas observadas en la familia se deben a un fenómeno de convergencia o por el contrario a un fenómeno de estasis morfológica. Un futuro análisis filogenético de los caracteres diagnósticos ayudaría a identificar la existencia de orígenes independientes para un mismo rasgo morfológico y por tanto aportaría la evidencia necesaria para refutar alguna de esas hipótesis.

Origen y diversificación del grupo

El modo de generación de la diversidad biológica subyace a un gran número de cuestiones evolutivas, particularmente relacionadas con el tiempo y diversificación de las especies. Distintas hipótesis han sido planteadas para intentar explicar los patrones de diversidad registrados a escala macroevolutiva, principalmente en base a observaciones directas del registro fósil (Raup, 1976). Así tres grandes hipótesis han sido planteadas: 1) crecimiento relativamente constante, 2) crecimiento constante con acumulación exponencial de linajes y puntuales extinciones en masa y 3) evolución a través de eventos de especiación explosivos (Benton y Emerson, 2007).

Desentrañar las relaciones filogenéticas en grupos donde se asume que ha acontecido un proceso antiguo y explosivo de especiación representa uno de los mayores desafíos de la sistemática actual, debido a la confusión que genera la escasez de caracteres sinapomórficos, el alto grado de homoplasia (morfológica y molecular) y la dificultad para evaluar el papel de la extinción (Jian *et al.*, 2008). Estos fenómenos de rápida diversificación han sido ampliamente documentados en grupos como plantas (Shaw y Renzaglia, 2004; Yoon *et al.*, 2006) y aves (Poe y Chubb, 2004), y aunque parecen ser muy comunes en crustáceos decápodos (Schram *et al.*, 1978; Morrison *et al.*, 2004; Porter *et al.*, 2005) son muy pocos los trabajos que han examinado estadísticamente dicha hipótesis.

En la familia Galatheidae, la falta de apoyo para resolver las relaciones filogenéticas tanto a nivel intra como intergenérico parece estar relacionada con el acontecimiento de un evento de rápida radiación durante el Mioceno (Machordom y Macpherson, 2004) por lo que uno de los objetivos específicos de la presente Tesis fue testar dicha hipótesis utilizando como modelo el género *Paramunida*. Para ello se exploraron cambios significativos (aceleración o deceleración) en las tasas de acumulación de linajes mediante el "relative cladogenesis test" (RC) (Rambaut *et al.*, 1997), modelos de supervivencia (Paradis, 1997) y "lineages through time" (LTT) (Pybus y Rambaut, 2002). Este tipo de metodologías, diseñadas para identificar cambios en las tasas de diversificación son sensibles al muestreo de especies; sin embargo, trabajos previos han mostrado que tienen suficiente precisión para detectar cambios significativos incluso en aquellas filogenias donde sólo se han muestreado la mitad de los taxones (Williams y Duda, 2008). Por lo tanto, y dado que para este trabajo fueron muestreadas aproximadamente el 82% de las especies del género, los resultados aquí presentados deberían de ser considerados robustos.

Todos los análisis llevados a cabo mostraron evidencias para concluir que el género *Paramunida* sufrió un evento de rápida especiación marcado por una serie de aceleraciones sucesivas en las tasas de diversificación, seguido de una disminución en las tasas de acumulación de linajes a lo largo del tiempo. Trabajos previos centrados en otros taxones marinos asociados a aguas superficiales (p.e. peces y moluscos) y con distribución Indo-Pacífica han detectado una señal filogenética similar (Read *et*

al., 2006; Alfaro *et al.*, 2007; Williams y Duda, 2008), por lo que nuestros resultados sugerirían que la diversificación de las faunas de aguas someras y profundas podría haber estado influenciadas por los mismos factores.

La escala temporal en la que se han enmarcado estos eventos de rápida cladogénesis abarca el período comprendido entre el Oligoceno-Mioceno. Las estimas de los tiempos de divergencia del presente trabajo mostraron un período similar para la diversificación del género *Paramunida*, con la detección de cinco incrementos en las tasas de diversificación desde comienzos del Oligoceno hasta mediados del Mioceno. Los intervalos de confianza de dichas estimas fueron amplios y por tanto deben ser interpretados con cautela. El registro fósil de decápodos es bastante escaso, y particularmente la familia Galatheidae tiene muy poca representación (De Grave *et al.*, 2009), por lo que no es posible evaluar el papel de la extinción en la historia evolutiva del grupo y además no pueden emplearse fósiles como puntos de calibración externos. De este modo, la aproximación a los tiempos de divergencia se realizó en base a las tasas de divergencia medias propuestas en otros crustáceos para genes como el ARNr 16S y el COI (Schubart *et al.*, 2000b; Stillman y Reeb, 2001; Lessios, 2008). Indudablemente, existe una fuente de error asociada al empleo de tasas propuestas para crustáceos que taxonómicamente están alejados del grupo objeto de estudio; sin embargo, hay que tener en cuenta que tasas similares han sido calculadas para crustáceos tan dispares como isópodos y braquiuros (Sturmbauer *et al.*, 1996; Ketmaier *et al.*, 2003).

Durante ese período de tiempo, la región experimentó eventos tectónicos de gran relevancia, como la colisión del margen norte de la placa Australiana con los arcos de la placa Euroasiática, lo que generó el movimiento y reorganización de los límites de las placas Pacíficas (Hall, 1998). Este hecho, en conjunción con la colisión de los arcos de Melanesia y la meseta de Java dieron lugar a la formación de la línea de Wallace, apertura de nuevas conexiones, así como un aumento en la complejidad de hábitats (Hall, 1998), lo que debió de promover la diversificación de la fauna marina (Williams y Duda, 2008). La intensa actividad tectónica de la época ha sido propuesta como el factor más determinante para explicar aceleraciones en las tasas de diversificación; sin embargo, procesos como alteraciones en el régimen de

temperatura global así como cambios en las corrientes oceánicas probablemente también fueron cruciales (Reaka *et al.*, 2008). Parece indudable que todos esos factores permitieron la extensión de hábitats someros como praderas de fanerógamas, sistemas arrecifales o manglares y la consiguiente diversificación de las faunas asociadas (Alfaro *et al.,* 2007; Reid *et al.*, 2009; Teske y Beheregaray, 2009), sugiriendo nuestros resultados que tales procesos también debieron afectar a las tasas de especiación de aquellos taxones distribuidos en aguas más profundas.

Los datos aquí presentados apoyan estadísticamente la existencia de un rápido evento de especiación durante el Oligoceno-Mioceno en el género *Paramunida*, y representan el primer intento por clarificar el origen y la diversificación de un linaje distribuido en aguas profundas del Pacífico. Sin embargo, estudios complementarios basados en otros taxones de aguas profundas son necesarios para constatar la existencia de un período y unas causas comunes para la diversificación de taxones asociados tanto a medios someros como profundos.

Reconstrucción de la historia biogeográfica

Como ya se ha destacado anteriormente, la región del "East-Indies Triangle" ha atraído la atención de los biólogos evolutivos desde tiempos históricos debido a que sus aguas concentran la mayor riqueza de especies marinas a nivel mundial. Son muchos los trabajos que han intentando identificar un proceso común generador de dicha diversidad; sin embargo, la existencia de una única explicación para ese patrón parece poco probable (Barber, 2009 y referencias citadas). De este modo, se han propuesto distintas hipótesis para explicar la generación de este centro de diversidad: 1) agregación de faunas procedentes de las distintas placas oceánicas (centro de solapamiento), 2) diversificación dentro del centro de diversidad (centro de origen) y 3) diversificación en los límites de distribución de las especies e invasiones secundarias del centro de diversidad (centro de acumulación).

En la presente Tesis Doctoral no hay suficientes datos como para poder inferir dichos procesos, y en ese sentido, son muy pocos los trabajos que han incorporado taxones de aguas profundas (> 200 m) a estudios biogeográficos, rechazando todos ellos la hipótesis de un único centro de especiación (Bouchet y

Kantor, 2004; Macpherson *et al.*, 2010). Concretamente para los galateidos de profundidad, el máximo de diversidad se localiza en las provincias marinas de Salomón, Vanuatu y Nueva Caledonia, con centros secundarios de diversidad en la regiones de Indonesia/Filipinas, Polinesia Francesa y Nueva Zelanda (Schnabel, 2009; Macpherson *et al.*, 2010). Este fenómeno podría ser resultado del mayor esfuerzo de muestreo llevado a cabo en la región de Nueva Caledonia y aguas adyacentes en comparación con otras regiones del Pacífico; sin embargo, tanto la riqueza de especies, como el elevado número de endemismos detectados en las diferentes regiones, sugieren la evolución independiente de cada una de ellas (Schnabel, 2009; Macpherson *et al.*, 2010).

En contraste, la reconstrucción biogeográfica llevada a cabo en el presente trabajo mostró únicamente un centro de diversificación para el género *Paramunida* en aguas del Pacífico Suroeste, concretamente en el arco de islas formado por Fiji, Tonga, Vanuatu y Wallis y Futuna. Posteriormente, el género se dispersó hacia el norte y este, colonizando Australia, Nueva Caledonia, las Islas Salomón, la Polinesia francesa y la región del Sureste Asiático. Este resultado podría deberse que se analizaron un mayor número de especímenes procedentes de esas localidades que de otras regiones del Pacífico como Indonesia o Filipinas. La falta de clados monofiléticos restringidos a un solo área así como el hecho de que la mayoría de especies hermanas se localizan en áreas diferentes apoyaría la existencia de un único centro de especiación; sin embargo, un muestreo más exhaustivo es necesario para poder constatar o refutar dicha hipótesis.

Por otro lado, nuestro estudio sugiere que la distancia geográfica no guarda una relación directa con el potencial de dispersión de los organismos marinos. De este modo, el modelo biogeográfico no restringido por distancia mostró un mejor ajuste a los datos que el modelo restringido. La gran mayoría de galateidos asociados con aguas profundas (>200 m) muestran un alto grado de regionalización, con distribuciones restringidas a islas o archipiélagos (Baba *et al.,* 2008). En claro contraste, los géneros asociados con aguas más superficiales muestran amplios rangos geográficos (p.e. *Allogalathea* o *Sadayoshia*), de este modo la especie *Allogalathea babai*

se distribuye en Japón, Indonesia, Nueva Caledonia y Australia, y la especie *Sadayoshia acroporae* Baba, 1972 se distribuye a lo largo del Indo-Pacífico.

En el medio marino, la ausencia de barreras geográficas claras al flujo génico en combinación con los elevados potenciales de dispersión de las larvas pelágicas, ha hecho que históricamente se asumiese una baja estructuración genética en poblaciones marinas (Palumbi, 1992); sin embago, son muchos los trabajos que muestran una falta de correlación entre ambos factores (Cowen y Sponauble, 2009 y referencias citadas). El limitado conocimiento sobre el desarrollo larvario en galateidos no permite concluir si tan llamativas diferencias entre galateidos de aguas superficiales y profundas pueden estar relacionadas con distintos potenciales dispersivos. Con los datos de los que disponemos actualmente, solamente puede hipotetizarse que factores alternativos como orografía marina, corrientes oceánicas o retención larvaria podrían tener un efecto diferencial sobre la fauna de galateidos de aguas someras y profundas.

Consideraciones futuras

El estudio de la biodiversidad marina en el Pacífico requiere integrar el conocimiento de la compleja historia geológica del área, así como aspectos de la sistemática, biología, ecología y biogeografía de las especies objeto de estudio. Desde un punto de vista taxonómico la familia Galatheidae ha recibido gran atención; sin embargo, la información disponible acerca de su biología y origen evolutivo es todavía muy limitada. El escaso registro fósil del grupo hace complicado evaluar el efecto de eventos históricos así como el papel de la extinción en el grupo, y por otro lado las diferencias en la intensidad de muestreo dificultan la interpretación de los patrones de distribución y diversidad de sus especies. A pesar de estas limitaciones, los resultados originalmente aquí mostrados tienen un gran valor en tanto que representan una base sólida sobre la que poder seguir progresando en el estudio de la historia evolutiva del grupo. Futuras investigaciones enfocadas a testar el valor filogenético de los caracteres morfológicos, en combinación con un mayor número de taxones, marcadores genéticos y tasas de sustitución más precisas, nos proporcionarán un mejor escenario para su interpretación.

Conclusiones

De los estudios presentados en esta Tesis Doctoral, pueden extraerse las siguientes conclusiones:

1. Los caracteres morfológicos asociados con la región epistómica así como algunos de la primera larva zoea representan una fuente adicional de caracteres taxonómicos y revelaron la existencia de un nuevo género para la Ciencia (*Babamunida).*

2. El estudio de los genes mitocondriales ARNr 16S y COI en combinación con caracteres morfológicos permitieron la descripción de una nueva especie para el género *Plesionida*, otra para el género *Agononida* y cuatro para el género *Munida*. Por otro lado, el análisis combinado de caracteres morfológicos y moleculares (genes mitocondriales y nucleares) apoyó el estatus taxonómico de los 13 nuevos linajes descritos para el género *Paramunida*.

3. Para el género *Paramunida* se destaca el valor taxonómico de los caracteres morfológicos asociados con la forma y longitud de los segmentos y espinas antenales y antenulares, la espinulación del caparazón, así como el tipo de estría y la distribución de las sedas a lo largo del surco cervical. Nuestros resultados sugieren la reexaminación de estos dos últimos caracteres en otros géneros de la familia con el objetivo de testar su utilidad taxonómica.

4. La heterogeneidad en los valores de divergencia genética entre las especies del género *Munida* así como la falta de apoyo de su monofilia destaca la necesidad de una profunda revisión del grupo. Asimismo, sería deseable un estudio más detallado del género *Agononida* con el objetivo de clarificar las sinapomorfías que definen el grupo, así como el estatus taxonómico de algunas de sus especies.

5. Se destaca la importancia de caracteres asociados con la forma y longitud de rostro así como la longitud, espinulación y distribución de las sedas en los pereiópodos para delimitar las nuevas especies descritas para el género *Allogalathea*. Asimismo, caracteres comúnmente empleados para la

identificación de galateidos como el número de epipodios en los pereiópodos así como su presencia/ausencia deberían de ser reexaminados puesto que presentan una alta variabilidad intraespecífica. Tanto los caracteres morfológicos como los moleculares apoyaron la descripción de tres nuevos taxones para el género.

6. El gen nuclear PEPCK no fue informativo para diferenciar las especies del género *Allogalathea*; sin embargo, datos preliminares no mostrados en la presente Tesis sugirieron un mayor poder de resolución para resolver las relaciones a nivel intergenérico.

7. Los genes mitocondriales COI, ARNr 16S y ND1 resultaron útiles para detectar variabilidad genética a nivel intra e intergenérico. No obstante, no fueron lo suficientemente informativos para resolver las relaciones evolutivas dentro de cada género y mostraron una falta de resolución en los nodos basales de las reconstrucciones filogenéticas.

8. El estudio combinado de los genes nucleares ARNr 18S y ARNr 28S mostró una señal filogenética similar a la de los genes mitocondriales, y aunque aportaron mayor resolución tampoco pudieron resolver completamente las relaciones evolutivas entre las diferentes especies del género *Paramunida*.

9. Nuestros resultados apoyaron la existencia de un rápido evento de diversificación en el género *Paramunida*, marcado por una serie de pulsos de rápida especiación, seguidos de una deceleración en las tasas de acumulación de linajes a lo largo del tiempo.

10. Los tiempos de divergencia mostraron que la diversificación del género *Paramunida* debió de acontecer durante el período de tiempo comprendido entre el Oligoceno-Mioceno; sin embargo, los amplios intervalos de confianza hacen necesario tomar dichas estimas con cautela.

11. La intensa actividad tectónica acontecida durante el Oligoceno-Mioceno en combinación con alteraciones en el régimen de temperatura global así como

cambios en las corrientes oceánicas debieron de promover la diversificación de las faunas marinas tanto de ambientes someros como profundos.

12. La región comprendida entre Tonga, Fiji, Vanuatu y Wallis y Futuna es propuesta como potencial área ancestral del género *Paramunida*. El grupo diversificó en la región Pacífico Suroeste y posteriormente se dispersó hacia el norte y este del Pacífico colonizando Australia, Nueva Caledonia, las Islas Salomón, la Polinesia Francesa y el Sureste de Asia.

13. La distancia geográfica no parece ser un buen criterio para definir tasas de dispersión en organismos marinos, puesto que el modelo biogeográfico no restringido por distancia mostró un mejor ajuste a los datos que el modelo restringido.

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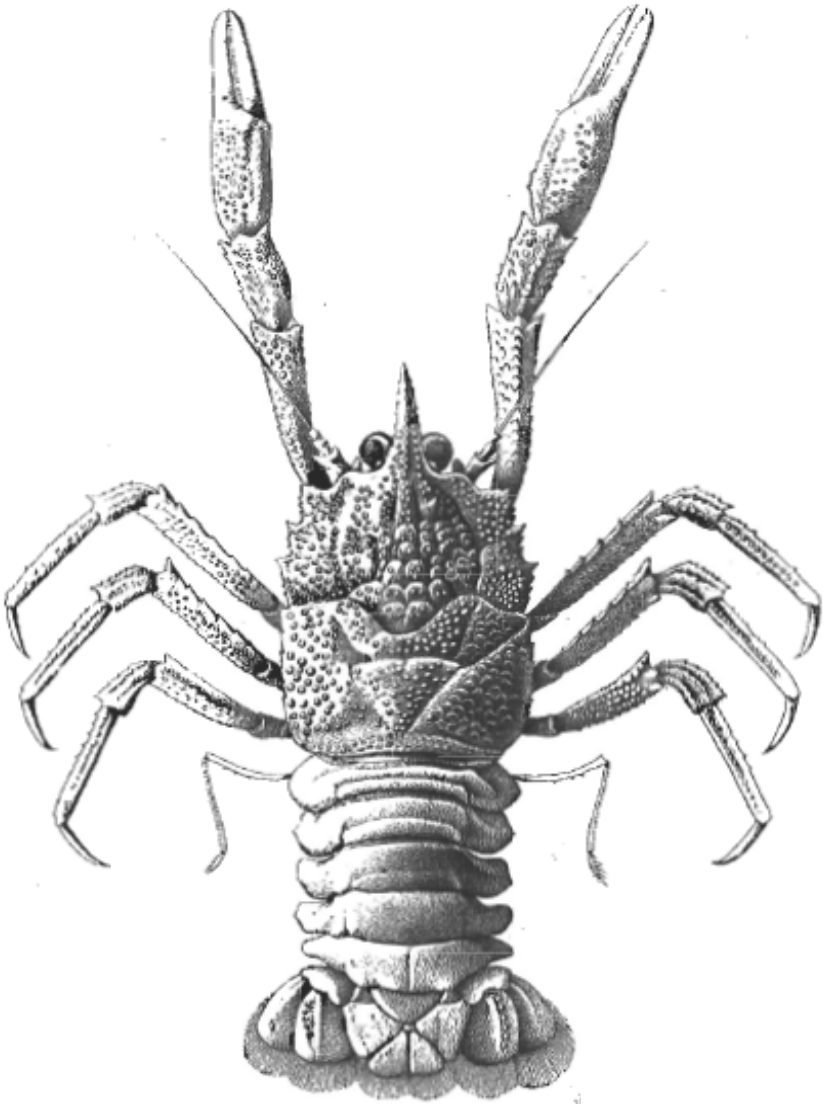

Munidopsis ornata Faxon, 1893

ANEXO I

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Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura—families Chirostylidae, Galatheidae and Kiwaidae)

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Table of contents

Abstract

Taxonomic and ecological interest in squat lobsters has grown considerably over the last two decades. A checklist of the 870 current valid species of squat lobsters of the world (families Chirostylidae, Galatheidae and Kiwaidae) is presented. The compilation includes the complete taxonomic synonymy and geographical distribution of each species plus type information (type locality, repository and registration number). The numbers of described species in the world's major ocean basins are summarised.

Key words: Crustacea, Decapoda, Anomura, Chirostylidae, Galatheidae, Kiwaidae, checklist, taxonomy

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Introduction

Crustaceans generally referred to as squat lobsters are members of three families of colourful anomuran decapods, the Chirostylidae, Galatheidae and Kiwaidae (Figs 1–4). Squat lobsters share with other Anomura the characteristic presence of five pairs of thoracic legs (pereopods). The first pair is elongate, slender and modified as pincers (chelipeds) and the next three pairs are shorter, simple, walking legs. The fifth pair is much smaller than the others, chelate, folded and usually hidden under the carapace. The general body plan is symmetrical and the abdomen is depressed. The uropods are spatulate, forming with the telson a broad tailfan, folding up against itself or the thoracic sternum. Adult males usually bear abdominal appendages (pleopods), the first one or two pairs of which are modified into copulatory structures known as gonopods. The first pair of female pleopods is always absent.

Squat lobsters are abundant, speciose and distributed worldwide. At the time of writing (May 2008) 870 species of squat lobsters are recognised (Table 1). They occur in all marine habitats, including anchialine caves and hydrothermal vent areas, and at depths ranging from the surface of the sea to more than 5000 m (Baba, 2005). Squat lobsters are primarily found in tropical and temperate waters but are scarce in high latitudes. All species are benthic although a few, such as *Munida gregaria*, can have pelagic juvenile forms (Williams, 1980). Few representatives of these families are economically important. Exceptions include several species from the Eastern Pacific (e.g., *Munida gregaria*, *Pleuroncodes monodon* and *Cervimunida johni* – see Tapella & Lovrich, 2006; Vinuesa, 2007) and off Europe (e.g., *Munida intermedia*). The ecological importance of squat lobsters, however, is unquestionable.

The Galatheidae are exceptionally diverse and include 675 species in 34 genera. The most speciose genera are *Munida* (243 species), *Munidopsis* (224) and *Galathea* (70). Most species of *Munida* are from shelf and slope depths. The majority of species of *Galathea* live in shallow waters whereas those of *Munidopsis* are found mainly on continental slopes and abyssal plains. Seventeen galatheid genera are exclusively found in the Pacific Ocean. In contrast, only one genus is found exclusively in the Atlantic Ocean (*Anomoeomunida*) and one in the Indian Ocean (*Nanogalathea*). Galatheid species are commonly found living in coral reef, rocky or muddy bottoms. Galatheids are found over the complete depth range of the oceans and in particular are the numerically dominant organisms collected in many shelf and slope benthic samples.

The Chirostylidae are also diverse and comprises seven genera and 192 species. *Uroptychus* (124 species) is the most speciose genus of this family. *Hapaloptyx*, a monospecific genus from off South Africa, is poorly defined taxonomically and needs further research. Representatives of most chirostylid genera are found in all oceans, with the exception of *Pseudomunida* and *Uroptychodes*, found exclusively in the Pacific Ocean, and *Hapaloptyx* restricted to the Indian Ocean. Chirostylids are typically deep-water animals from the continental slope or abyssal depths and often are associated with corals such as antipatharians, alcyonaceans and gorgonaceans.

The Kiwaidae are known only from one species *Kiwa hirsuta* (the 'yeti lobster'), but a second undescribed species is known. *Kiwa hirsuta* was collected at hydrothermal vent sites in the southeastern Pacific and to date kiwaids are only known from this habitat (Macpherson *et al.*, 2005).

The systematic placement of squat lobster taxa continues to be debated as families, genera and species become better defined. Previously, the Chirostylidae and Galatheidae, together with family Porcellanidae (porcelain crabs) were grouped in the superfamily Galatheoidea (Martin & Davis, 2001). The single species of Kiwaidae was placed in its own superfamily Kiwaoidea by McLaughlin *et al.* (2007). However, more recent phylogenetic appraisals suggest that Kiwaidae and Chirostylidae are more closely related to hermit crabs than to the Galatheidae and that galatheids are related more to Porcellanidae (Chu *et al.*, in press; Ahyong *et al.*, in press).

TABLE 1. Number of species by genus of the three families of squat lobsters tabulated by major ocean basin. Note that some species can be found in more than one ocean, therefore the total number of species can be different from the total number of known species. Furthermore, those species cited in Southern Ocean are included in the Indian and Pacific Oceans.

	Total species	Atlantic Ocean	Indian Ocean	Pacific Ocean
Chirostylidae				
Chirostylus	6		1	5
Eumunida	28	3	3	23
Gastroptychus	21	5	2	16
Hapaloptyx	1		1	
Pseudomunida	1			1
Uroptychodes	11			11
Uroptychus	124	18	36	79
Total Chirostylidae	192	27	43	135
Galatheidae				
Agononida	31	2	2	27
Alainius	1			1
Allogalathea	1			1
Allomunida	1			1
Anomoeomunida	1	1		
Anoplonida	3			3
Babamunida	5		1	4
Bathymunida	14		1	13
Cervimunida	2			2
Coralliogalathea	1		1	1
Crosnierita	4			4
Enriquea	1			1
Fennerogalathea	2		1	1
Galacantha	9	4	4	7
Galathea	70	15	22	43
Heteronida	3			3
Janetogalathea	1			1
Lauriea	2		1	2
Leiogalathea	2	1		1
Munida	242	43	26	176
Munidopsis	224	71	50	132
Nanogalathea	1		1	
Neonida	1			1
Onconida	5			5
Paramunida	23		1	22
Phylladiorhynchus	5		4	3
Plesionida	2			2
Pleuroncodes	2			2

Raymunida	10		2	9
Sadayoshia	2		1	2
Setanida	1			1
Shinkaia	1			1
Tasmanida	1			1
Torbenella	3			3
Total Galatheidae	677	138	118	476
Kiwaidae				
Kiwa	1			1
Total Kiwaidae	1			1
Total all families	870	164	161	612

Given such high diversity within the group, it is not surprising that squat lobsters have a rich taxonomic history. Baba (2005) has discussed this history in detail; his publication is available on the website of the *Galathea Reports http://www.zmuc.dk/inverweb/Galathea/Galathea_p5.html.*

Baba's (2005) catalogue and keys dealt only with species of the Indo-West Pacific occurring at slope depths (>200 m). The present contribution covers all oceans and all depths.

The cumulative curve of new species described over time is not flattening out, and suggests that the diversity of these families is still far from being well-known (Figure 5). The great exploratory expeditions carried out in the last quarter of the nineteenth century – H.M.S. *Challenger* on its round-the-world voyage, H.M. Indian Marine Survey Steamer *Investigator* in the Indian Ocean, U.S. Fish Commission Steamer *Albatross* in the Pacific, and U.S. Coast Survey Steamer *Blake* in the Atlantic – provided a wealth of material for taxonomists describing new species. The rate of description of new taxa was relatively low during the first half of the twentieth century but several expeditions, e.g., by vessels such as *Albatross*, *Valdivia* and *John Murray*, provided extensive new material. However, the most important advances in the taxonomy of these families occurred after the large and complete revisions made by Baba (1988, 2005) based on the *Albatross* expeditions to the Philippines and Danish research ship *Galathea* worldwide. More recently, numerous expeditions, mainly in the western Pacific, have discovered a large number of new genera and numerous new species. This catalogue is not the last word. Many more species are in the pipeline, including c. 100 new chirostylids (Baba and Schnabel; Schnabel, in press), new species of *Eumunida, Uroptychus, Munida*, *Paramunida*, *Plesionida* and *Agononida* from Taiwan (Lin *et al.*), new species of *Munidopsis* from the South Atlantic (Rodrigues), new taxa from the Solomon Islands (Cabezas *et al.*), NW Africa (Baba & Macpherson), New Zealand (Ahyong), North Atlantic and Gulf of Mexico (Nizinski), and c. 70 undescribed species from Western Australia (some listed by Poore *et al.*, 2008).

Relationships between the species have received attention from molecular systematists, notably to elucidate population structure (Creasy *et al.*, 2000), to confirm the systematic status of *Raymunida* and its species (Macpherson & Machordom, 2001), to unravel sibling species of *Munida* (Macpherson & Machordom, 2005), to propose new genera (Machordom & Macpherson, 2004; Cabezas *et al.*, 2008) and to support the description of new species of *Munidopsis* (Cubelio *et al.*, 2007a; Jones & Macpherson, 2007). Molecular studies of galatheids contributed to a study of endemism on seamounts (Samadi *et al.*, 2006). And the description of the new family Kiwaidae depended in part on molecular characterisation (Macpherson *et al.*, 2005).

This paper arose out of work begun during the week 3–7 September 2007 when we ten taxonomists of squat lobsters met at the National Institute of Water and Atmospheric Research, Wellington, New Zealand, to coordinate research and to compile taxonomic resources (species list, bibliography, electronic keys, electronic

library) to publish on the web. The workshop was supported by COMARGE (Continental Margin Ecosystems) (http://www.ifremer.fr/comarge/en/index.html), one of fourteen Census of Marine Life (CoML http://www.coml.org/) field projects dedicated to the description and understanding of biodiversity patterns on continental margins. Continental margins refer here to the deep-sea realm comprising between about 200 meters and 4000 meters depth. The overall aim of COMARGE is to describe biodiversity patterns on continental margins at different spatial scales and identify the contributions of environmental heterogeneities to these patterns. To achieve its goals, COMARGE is creating a network of researchers to facilitate coordination among projects and cruises, to foster data sharing, to support data archiving and finally to assure the maximum synergistic value for continental margin studies. This paper is the first step along this path for one group of crustaceans that dominate on continental margins.

The aim of this paper is to clarify the status of all available squat lobster species names by listing them in an accepted taxonomy with their synonyms. Type data (nature and depository of types) and type locations are presented for each accepted species. Other significant citations with taxonomic or distributional content are also given along with reported locality records. The species list does not include fossil species nor are palaeontological references included.

Numerous ecological, physiological and parasitological papers are not cited. The bibliography of papers cited, 672 in all, are 68% of all the titles accumulated as part of our endeavours. All titles, many with accompanying pdfs, have been deposited at the Assembling the Tree of Life - Decapoda website (http://decapoda.nhm.org/) where they can be downloaded in Endnote X® format.

Museum and collection acronyms

AHF	Allan Hancock Foundation, Los Angeles
AM	Australian Museum, Sydney
BLIH	Biological Laboratory, Imperial Household, Tokyo
BMBN	Bergen Museum, Bergen,
BMNH	Natural History Museum (formerly British Museum (Natural History)), London
BOC	Bingham Oceanographic Collection, New Haven
BPBM	Bernice P. Bishop Museum, Honolulu
CMNH	Coastal Branch of Natural History Museum and Institute, Chiba
EMU	Estación Mazatlán, Universidad Nacional (UNAM), Mazatlán
ICM	Instituto de Ciencias del Mar (CSIC), Barcelona
KU	Kumamoto University, Kumamoto
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCSN	Museo Civico di Storia Naturale, Milan
MCZ	Museum of Comparative Zoology at Harvard University, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHNC	Museo Nacional de Historia Natural, Chile, Santiago
MNHNL	Museu Nacional Historia Natural, Lisbon
MZS	Museé Zoologique, Strasbourg
MZUSP	Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo
NFUS	National Fisheries University, Shimonoseki
NIWA	National Institute of Water and Atmospheric Research (formerly New Zealand Oceanographic Institute), Wellington
NMCR	National Museum of the Philippines, Manila
NMNZ	National Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand
NMV	Museum Victoria (formerly National Museum of Victoria), Melbourne

NMW	Naturhistorisches Museum, Vienna
NSMT	National Science Museum, Tokyo
NTOU	National Taiwan Ocean University, Keelung
OIRAS	Oceanology Institute, Russian Academy of Sciences, Moscow
QM	Queensland Museum, Brisbane
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie te Leiden), Leiden
SAMA	South Australian Museum, Adelaide
SAMC	South African Museum, Cape Town
SCSFRI	South China Sea Fisheries Research Institute, Guangzhou
SIO	Scripps Institution of Oceanography, La Jolla
SMF	Senckenberg Museum, Frankfurt am Main
SMNH	Swedish Museum of Natural History, Stockholm
SNU	Seoul National University, Seoul
SUM	State University of Moscow, Moscow
TMH	Tasmanian Museum and Art Gallery, Hobart
USNM	National Museum of Natural History, Washington, D.C.
USU	Universidade Santa Ursula, Rio de Janeiro
ZLKU	Kitakyushu Museum of Natural History, Kitakyushu
ZMA	Zoological Museum, Amsterdam
ZMB	Zoologisches Museum, Zentralinstitut der Humboldt-Universität, Berlin
ZMG	Zoologische Museum, Göttingen
ZMM	Zoological Museum, Moscow State University, Moscow
ZMUC	Zoological Museum, Copenhagen
ZRC	Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore
ZSIC	Zoological Survey of India, Calcutta
ZSM	Zoologische Staatssammlung, Munich

Contributions of the authors

The checklist and associated information were generated from a database maintained by the first two authors, Keiji Baba and Enrique Macpherson. Gary Poore convened the workshop, maintained the Endnote® bibliographic database with many contributions from others, and edited this manuscript. The other authors, listed alphabetically, attended the workshop, helped with the coordination of data from numerous sources and contributed valuable details.

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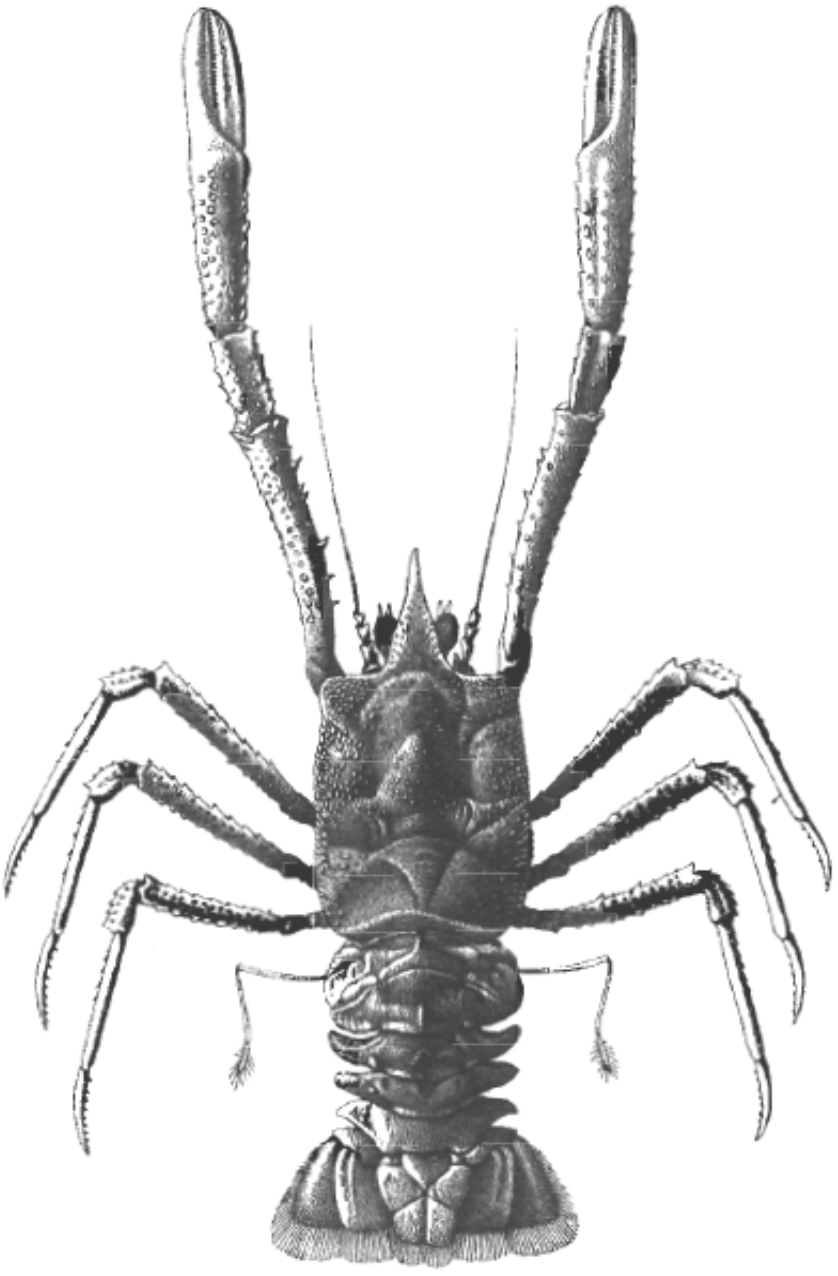

Munidopsis quadrata Faxon, 1893

ANEXO II

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TECHNICAL NOTE

Development and characterization of microsatellite markers for the endangered anchialine squat lobster *Munidopsis polymorpha*

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Abstract Species of the genus *Munidopsis* are typically distributed in bathyal and abyssal zones, but the anchialine species *Munidopsis polymorpha* is an exception. It inhabits a volcanic tube on Lanzarote Island (Canary Islands, NE Atlantic) and is currently listed as endangered due to its highly restricted distribution and degree of endemism. Microsatellite loci were isolated from partial genomic libraries that had been enriched for AC, ACAG, GATA, AAAC and AAG repeat sequences. Eight loci were polymorphic in a sample of 24 individuals. The number of alleles per locus ranged from 2 to 4 with observed and expected heterozygosities ranging from 0.083 to 0.875 and from 0.080 to 0.681, respectively. These markers will be used to evaluate levels of genetic diversity and inbreeding, providing essential information for the development of a management and conservation strategy for this species.

Keywords Canary Islands · Endangered species · Microsatellites · *Munidopsis polymorpha*

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Anchialine habitats are defined as pools with no surface connection to the sea that contain salt or brackish waters that fluctuate with tides due to the proximity to the coast (Holthuis 1973). Such habitats have a worldwide distribution and a rich invertebrate fauna, mainly dominated by crustaceans (Iliffe 2000). The squat lobster *Munidopsis polymorpha* is a typical anchialine species. Although it is considered to be restricted to a volcanic tube on Lanzarote Island (Canary Islands, NE Atlantic), isolated specimens have been reported in saline wells close by (González-Pérez 1995), and unconfirmed data suggest that it may also be present on Hierro Island, in the west of the archipelago. Despite the fact that this species is classified as in danger of extinction because of its highly restricted distribution and degree of endemism (Templado et al. 2004) no studies have been carried out to evaluate its genetic conservation status. The development of a management strategy for this species requires information from rapidly evolving and variable nuclear markers such microsatellites, which can provide essential information pertinent to both the conservation genetics and the evolution of the species (Frankham et al. 2002). Here, we report the development and characterization of the first microsatellite loci for studying genetic structure in the endangered galatheid squat lobster *M. polymorpha*.

A genomic library was constructed with total DNA extracted from muscle tissue from a single pereiopod. Microsatellite loci were isolated using an enrichment protocol from Bloor et al. (2006) with minor modifications. Approximately 4.6 μg of genomic DNA was digested with 50 U of *MboI* restriction enzyme (Invitrogen). The quantity of restriction enzyme used was 10 times higher than recommended to ensure complete or almost complete digestion. The digested DNA was subsequently ligated to site-specific adapter (Refseth et al. 1997) and fragments

Table 1 Description of the eight microsatellites isolated from *Munidopsis polymorpha*

Locus	Primer sequence (5′–3′)	Repeat motif	Size of cloned allele (bp)[a]	N	N_A	H_0	H_E	GenBank (Accesion no.)
Mp-1	F: *HEX*- TTCCACAATGAGCACTGGAC	$(CTAT)_{16}$	350	24	4	0.292	0.294	EU597332
	R: GCATATGTGGAGCCTGGATT							
Mp-2	F: *6-FAM*- GGAGAGGGAGTTATCGAGAGG	$(CTAT)_{15}TTAT(CTAT)_6$	249	24	3	0.500	0.497	EU597333
	R: GGGGAGTCTGGAATTAAATGG							
Mp-3	F: *NED*- CGTCTTTGGCTGCGACTAA	$(TATC)_{15}$	293	24	3	0.125	0.119	EU597334
	R: ACGGCGTCAGGCAATAAATA							
Mp-4	F: *6- FAM*- TGACCAAACAAATATTCCTTAGTAGG	$(GATA)_{13}$	154	24	2	0.417	0.444	EU597335
	R: CTCATGTGGGCCTCTGAATA							
Mp-5	F: *HEX*- TCGTGCTTCTCTTTCAATGC	$(TATC)_{34}$	296	24	2	0.083	0.080	EU597336
	R: ACAATGGGAATGAGGGGAAG							
~Mp-6	F: AACCTCTCCTTGCCTTCCTT	$(TTTG)_9$	236	24	3	0.083	0.081	EU597337
	R: TCGTTGGCAGAGGTAACAAAC							
Mp-7	F: *6- FAM*- CTCCAGGCACAGATACTGACAC	$(TG)_{17}$	301	24	4	0.875	0.681	EU597338
	R: GGTGATGACTGAACACAAGTCC							
~Mp-8	F: AGCATCAATTCTGCCCTTTC	$(TCCA)_4(TCTA)_9(TC)_2(TATC)_{10}$	189	23	4	0.348	0.300	EU597339
	R: GATCACCCCACTTGAAGGAA							

Primer sequence, repeat motif, size of cloned allele, sample size (N), number of alleles (N_A), observed heterozygosity (H_O), expected heterozygosity (H_E) and GenBank accession numbers are given

[a] Based on the GeneScan500 size standard

~Mp-6 and ~Mp-8 were fluorescently end-labelled with 6-FAM by reamplification using a protocol modified from Schuelke (2000) with the oligonucleotide primer PaulAn (5′-TGACGACCCCATGCTACG-3′) from Acevedo et al. (2008)

R, All reverse primers, excepting Mp-7R, were "PIG- Tailed" with 5′-GTTTCTT-3′ (Brownstein 1996) to facilitate genotyping

between 300 and 1,200 bp excised from a 2.5% agarose gel (Biotools Gel Extraction), discarding any incompletely digested genomic DNA. Subtractive hybridization was carried out with 200 pmol of 3′-biotinylated repeated oligos $(AC)_{10}$, $(ACAG)_6$, $(GATA)_6$, $(AAAC)_6$, $(AAG)_8$ bound to streptavidin-coated beads (Dynabeads M-280, Invitrogen). Subtractive hybridization was carried out separately for each oligo. Enriched DNA was amplified by polymerase chain reaction (PCR), ligated into pGEM-T vector (Promega) and then used to transform *Escherichia coli* competent cells (TOPO TA Cloning, Invitrogen). Recombinant colonies were identified by blue/white screening on agar/ampicillin/IPTG/X-gal plates. Microsatellite containing colonies were identified by the presence of at least two amplification products after colony PCR using oligo A (Refseth et al. 1997) and a corresponding repeat-sequence oligo as primers. Inserts of positive clones were sequenced on an ABI PRISM 3730 DNA Sequencer (Applied Biosystems) and analyzed using the program SEQUENCHER 4.6 (GeneCode). Of a total of 156 positive clones sequenced, 73 contained repeat sequence. Of these, 19 were chosen for primer design. The remaining sequences were discarded due to the presence of very irregular and/or very long repeat sequences. The hybridization capture with tetranucleotide repeat sequences yielded the greatest number of positive clones relative to the di or trinucleotide repeat sequences. Primers were designed using the PRIMER 3 software (Rozen and Skaletsky 2000). Primer pairs were first tested by typing a sample of eight individuals. The forward primer from each pair was fluorescently end-labelled either directly with 6-FAM, HEX or NED or indirectly by reamplification using a protocol modified from Schuelke (2000) (Table 1). Reverse primers were "PIG-Tailed" (Brownstein et al. 1996) to facilitate genotyping (Table 1). Amplifications were carried out in 15-μl reaction volumes: 1× standard reaction buffer with a final concentration of 2.0 mM $MgCl_2$, 0.2 mM of each dNTP, 0.75 μM of each primer, 0.5 U *Taq* polymerase (Biotools) and 1–8 ng of DNA (extracted using ChargeSwitch gDNA Micro Tissue Kit, Invitrogen). The cycling profile was 94°C for 4 min, followed by 35 cycles at 94°C for 30 s, 56°C for 30 s and 72°C for 45 s. Fluorescently labelled PCR products were run on an ABI PRISM 3730 DNA Sequencer (Applied Biosystems) with the GeneScan500 internal size standard and analysed with the GeneMapper software (Applied Biosystems).

Of the 19 microsatellites tested, seven could not be unambiguously scored and four were monomorphic (GenBank Accesion nos. EU597340-EU597343). The remaining eight loci were deemed useful (GenBank Accesion nos. EU597332-EU597339). Levels of polymorphism were determined by typing a sample of 24 individuals. Number of alleles (N_A), observed (H_O) and expected (H_E) heterozygosities were calculated with the program GENEALEX 6.0 (Peakall and Smouse 2006). Tests of Hardy–Weinberg equilibrium and linkage disequilibrium were carried out using the program GENEPOP 3.4 (Raymond and Rousset 1995, http://genepop.curtin.edu.au/) using 1,000 dememorizations with 100 batches (1,000 iterations per batch). Significance levels ($\alpha = 0.05$) were adjusted for multiple comparisons using the sequential Bonferroni correction (Rice 1989). A total of 25 alleles (2–4 alleles per locus) were detected across the eight loci in the sample of 24 *M. polymorpha* individuals typed (Table 1). Observed and expected heterozygosities ranged from 0.083 to 0.875 and 0.080 to 0.681, respectively (Table 1). No significant deviations from Hardy–Weinberg equilibrium were found, and none of the loci showed linkage disequilibrium after applying the sequential Bonferroni correction (Rice 1989). The polymorphic microsatellite loci presented here will be used to study genetic structuring in *M. polymorpha*, providing important information for a future conservation and management strategy for the species.

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