On the Origin and Evolution of True Crabs: Insights from Tropical America

by

Javier Luque

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
SYSTEMATICS AND EVOLUTION

Department of Biological Sciences
University of Alberta

Abstract

A full understanding of the evolution of novel forms requires inference about their origins through the study of variation in extant taxa and clues from the fossil record. However, the origins of morphological diversity in many groups are obscured by the scarcity of transitional fossils or reliable early occurrences of crown groups near the base of major branches. This is the case for true crabs, or Brachyura, a group whose evolutionary history and internal phylogenetic relationships remain unresolved. Although molecular and morphological phylogenetics bring powerful tools to the study of relatedness at the genotypic and phenotypic levels, the fossil record provides a unique glimpse into the origins of such relatedness by revealing a past morphological diversity otherwise inaccessible. Furthermore, fossils are pivotal for understanding the evolution of key traits, and provide geographic and chronologic data critical to the calibration of nodes of interest. Unfortunately, in spite of the overall good crab fossil record in Late Cretaceous and Cenozoic deposits worldwide, records of early brachyurans are still poorly known, and a strong collection bias towards modern high latitudes limits our understanding of the origins of the group's origin and early morphological variation.

Here I examine the fossil record of true crabs from the tropical Americas based on newly discovered crustacean-rich assemblages from the Early and 'mid' Cretaceous and re-examination of museum specimens, with emphasis on some brachyuran higher taxa (e.g., Raninoida, Eubrachyura, and a new chimaeric lineage described herein). I test hypotheses about the relationships among the main fossil brachyuran lineages, and investigate the distribution of visual systems in 'intermediate' brachyuran groups. Analyses of morphological data from fossil and extant taxa support the view that podotreme brachyurans (crabs with sexual openings at the base of the legs) form a paraphyletic grade, and that some derived podotreme groups might be closer to Eubrachyura or ‘higher’ true crabs than to less inclusive podotremes. New Cretaceous fossils push the envelope for what a ‘crab’ is, and challenge conventional views of crab evolution. My findings show that the evolution of shovel-like and paddle-like pereiopods, and decarcinization, or loss of a typical ‘crab-like’ form, have occurred independently at least five times since the Early Cretaceous or before. Similarly, my findings reveal that the loss of the plesiomorphic ‘mirror’ eyes — seen among most decapod crustaceans including the earliest brachyurans — has occurred in several podotremes and in eubrachyurans since at least the Early Cretaceous. In addition, the distribution of eye types among brachyuran crabs supports a paraphyletic podotreme grade, as suggested by recent phylogenetic works. The versatility of the crab body form, and the interplay between development and ecological invasion, may have acted as drivers of morphological innovation. These findings provide novel insights about the time, place, and phylogenetic pathways of early diversification in crabs, with the aim of contributing to the vast ongoing inter–institutional effort to resolve the Decapoda Tree of Life.

Preface

Chapter 2 has been published as Luque, J. *(2015)* The oldest higher true crabs (Crustacea: Decapoda: Eubrachyura): insights from the Early Cretaceous of the Americas. *Palaeontology* **58**(2): 251–263. http://onlinelibrary.wiley.com/doi/10.1111/pala.12135/full.

Chapter 3 has been published as Luque, J. *(2015)* A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: frog first or crab first? *Journal of Systematic Palaeontology* **13**(2): 153–166 http://dx.doi.org/10.1080/14772019.2013.871586.

Chapter 4 is near submission as Luque, J., Feldmann, R.M., Vernygora, O., Schweitzer, C.E., Cameron, C.B., Kerr, K.A., Vega, F.J., Duque, A., Strange, M., Palmer, A.R., & Jaramillo, C. Exceptional preservation of a chimaera crab from the Cretaceous unveils the evolution of a novel body form. J.L. conceived and designed the study, discovered the Colombian material, prepared the specimens, studied and described the material. M.S. discovered the US material. J.L., R.M.F, C.E.S. constructed the dataset. J.L., O.V., C.B.C. analyzed the data. A.D. designed the digital reconstructions and 3D animations. R.M.F., C.E.S., K.A.K., C.B.C., A.R.P., C.J. contributed logistics/materials/analysis tools. J.L. wrote the paper and made the line drawings, figures, and tables. O.V. made the Supplementary Figures S4.8 and S4.9. J.L., K.A.K., R.M.F., C.E.S., O.V., F.J.V., C.B.C., A.R.P., C.J. edited the manuscript.

Chapter 5 has been published as Luque, J., Schweitzer, C.E., Santana, W., Portell, R.W., Vega, F.J., and Klompmaker, A.A. *(2017)* Checklist of fossil decapod crustaceans from tropical America, Part I: Anomura and Brachyura. *Nauplius* **25**: e2017025 https://doi.org/10.1590/2358-2936e2017025. JL conceived and designed the study, analyzed the data, wrote the paper, and made Figures 5.1–5.4, 5.6–5.10, and Chart 5.17. WS made a draft of Figure 5.5; RWP a draft of Figures 5.11, 5.12, 5.14–5.16; and FJV a drat of Figure 5.13. JL edited and All authors contributed data and edited the manuscript.

Chapter 6 is a work in progress, and aims to be a mixed review and data paper about the distribution of visual systems in fossil and extant true crabs.

Dedication

In memory of my father, who always encouraged me to follow my dream of becoming an '-ologist' (geologist, biologist, palaeontologist). To my mother, who together with my father, instilled in me a deep passion and appreciation for nature, and for never getting mad at me for bringing home every possible rock and dead critter I found in our camping trips in the Andes. Their constant support and encouragement paved the road I walk today. To Livia, my best furry friend, who I dearly miss every day, and to Sailor and Mona (a.k.a. Sweet Pea), for bringing so much joy to our lives (pure entertainment). And especially to Kecia, the sun of my life, whose shining light illuminates my steps. To them, my eternal gratitude, my eternal love.

Acknowledgements

This work was possible thanks to the generosity of several sources that provided partial funding during the tenure of my PhD, in particular the Natural Science and Engineering Research Council of Canada (NSERC) Canada Graduate Scholarship (CGS–D), the Izaak Walton Killam Memorial Scholarship, the Andrew Stewart Memorial Graduate Prize, the University of Alberta President's Doctoral Prize of Distinction, the Devendra Jindal Graduate Scholarship, the Alberta Society of Professional Biologists Graduate Scholarship, and the Kay Ball Memorial Graduate Student Research Travel Award (Canada). Additional support was provided by the NSERC Discovery Grant A7245 and RGPIN 04863 to A. Rich Palmer. Thanks also to the Smithsonian Tropical Research Institute Short (Panama), the Fondo Corrigan-ACGGP-ARES (Colombia), the Sedimentary Geology, Time, Environment, Paleontology, Paleoclimatology & Energy (STEPPE) and the National Science Foundation (NSF) Student Travel Award Grant (USA).

Special thanks to Carlos Jaramillo, one of my mentors, and who has supported much of my research and fieldwork during my career. To Chris Cameron, also a mentor and friend, thanks to whom I ended up coming to the University of Alberta for my Ph.D. To John Christy, Rodney Feldmann and Carrie Schweitzer, Francisco Vega, Barry van Bakel, Àlex Ossó, Danièle Guinot, Roger Portell, Austing Hendy, Adiël Klompmaker, William Santana, Thomas Hegna, and Jo Wolfe for their friendship and intellectual support. Thanks to Prof. Fernando Etayo-Serna, to Roberto Terraza, and Diana Montoya, for field support and information regarding the stratigraphic position of the material studied in Chapter 2. To Alessandro Garassino, Hiroaki Karasawa, and John E. Simes, for providing images of type specimens illustrated in Chapter 2. To Paula Sucerquia, Rodney Feldmann, Barry Van Bakel, and Roger Portell, for thoughtful discussions and providing photos of specimens illustrated in Chapter 3. To John Maisey, Lorraine Meeker and Chester Tarka, for the photos of the Cretaceous brachyuran larva illustrated in Chapter 3. To Christopher Boyko, Arthur Anker, Tin Yam Chan, and Hans Hillewaert for some of the images of extant crabs illustrated in Chapter 4. To Sylvain Charbonnier, Jocelyn Falconnet, Peter Massicard, Rodney Feldmann, Roger Portell, Sean Rogers, Francisco Vega, and William Santana, for providing images of fossil specimens illustrated in Chapter 5.

To Gale Bishop, Bruce Thiel, Àlex Ossó, and Rick Ross, for their enormous generosity providing literature and reference materials. To Jose Arenas, Mauricio Pardo, and the Colombian Geological Survey, for providing export permits and field support. To Rafael Lemaitre, Karen Reed, and Daniel Levin, for help accessing the United States National Museum of Natural History (Smithsonian Institution) Zoology and Palaeobiology collections. To Peter Davie, for help accessing the QMW Invertebrate Zoology collections at the Queensland Museum, Brisbane, Australia. To Roger Portell for help accessing the Invertebrate Paleontology collections at the Florida Museum of Natural History, University of Florida, Gainesville, Florida. To Sylvain Charbonnier, Paula Martin-Lefebre, and Laure Corbaire, for help accessing the Palaeontology and Invertebrate Zoology collections at the Muséum national d'Histoire naturelle, Paris, France. To the Autoridad del Canal de Panamá (ACP) for providing laboratory facilities; the Dirección de Recursos Minerales de Panamá for facilitating collecting and export permits; Ricardo Perez for donating the Toyota vehicles used for fieldwork in Panama. To Arelene Oatway, Nathan Gerein, and Jorge Ceballos, for microscopy lab assistance.

Thanks to Jorge Moreno, Alexis Rojas, Dayana Schonwalder, Juan Camilo Villegas, Jaime Castellanos, Carlos Romero, Cesar Silva, Nicolás Pérez, Alejadra Rodríguez-Abaunza, Dirley Cortés, and numerous friends and colleagues from the Center for Tropical Paleoecology and Archaeology (CTPA, Smithsonian Tropical Research Institute, Panama) for field assistance. To Milton Rueda, Doña Rebeca Rueda, Luis Felipe Guarín, Luis Herrera and Doña Rosalbina de Herrera , Mary Luz Parra-Rugue, Juan de Dios Parra, Oksana Vernygora, and Alison Murray, for their friendship, hospitality, and field assistance. To Louise Haan, Brian Kopach, Lois Hammond, Oksana Vernygora, Nicole Webster, Tiago Simoes, Ilaria Paparella, Paulina Jimenes-Huidobro, Aaron Leblanc, Aaron Lechelt, Crysta Melvin, for being incredible sources of energy and happines during my Ph.D.

Finally, my sincere thanks to my committee members Rafael Lemaitre and Heather Proctor for their continuous support, encouragement, and friendship since the beginning of my degree. Especially, my most profound thanks to A. Rich Palmer, my supervisor, for whom I have an inmense debt of gratitute for his guidance, mentorship, generosity, friendship, and encouragement. This work would have never been possible without his support. From Rich I have learned several golden lessons, to remain curious and brave, and to go where the mess is.

Table of Contents

Preface iv

Dedication v

Acknowledgements vi

Table of Contents viii

List of Tables xii

List of Figures xiii

List of Abbreviations xv

  Anatomical and phylogenetical abbreviations xv

  Institutional abbreviations xvi

Chapter 1. General introduction 1

 1.1. Systematic relationships among brachyuran crabs 2

 1.2. The roots of Eubrachyura 3

 1.3. The early origins of Raninoida 4

 1.4. Novel forms in the fossil record 5

 1.5. The fossil record of crabs in the tropical Americas 6

 1.6. Diversity of visual systems in crabs and their phylogenetic significance 6

Chapter 2. The oldest ‘higher’ true crabs (Crustacea: Decapoda: Brachyura): Insights from the Early Cretaceous of the Americas 12

 2.1. Introduction 12

 2.2. Geological setting 13

 2.3. Material and methods 14

 2.4. Results 14

  2.4.1. Systematic palaeontology 14

 2.5. Discussion 24

 2.6. Conclusions 25

Chapter 3. A puzzling frog crab (Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: Frog first or crab first? 31

 3.1 Introduction 31

 3.2. Results 32

  3.2.1. Systematic palaeontology 32

  3.2.2. Phylogenetic analysis 35

3.3. Discussion 36
3.4. Conclusions 39
Chapter 4. Exceptional preservation of a chimaera crab from the Cretaceous reveals a novel body form and mode of life in early crabs 46
4.1 Introduction 46
4.2. Materials and methods 48
4.2.1. Origin of specimens 48
4.2.2. Phylogenetic analyses 48
4.3. Results 49
4.3.1. Systematic paleontology 49
4.4. Discussion 58
4.4.1. Heterochronous development of the chimaeric body plan 58
4.4.2. Convergence of paddle limbs in aquatic euarthropods 60
4.4.3. Phylogenetic and evolutionary implications. 61
4.5. Supporting Methods 68
4.5.1. Fossil specimens and preparation 68
4.5.2. Microscopy, photography, measurement and illustration 68
4.5.3. Phylogenetic analysis 69
4.6. Supplementary Text 71
4.6.1. Geographical and geological settings 71
4.6.2. Supplementary taxonomic remarks 73
4.6.3. Supplementary systematic remarks 74
4.6.4. Additional remarks 76
Chapter 5. Checklist of fossil decapod crustaceans from Tropical America, Part I: Anomura and Brachyura 88
5.1. Introduction 88
5.2. Annotated checklist 90
5.3. Northern South America 90
5.3.1. Bolivia 90
5.3.2. Brazil 92
5.3.3. Chile 99
5.3.4. Colombia 102
5.3.5. Ecuador 107

5.3.6. Peru 108
5.3.7. Venezuela 110
5.4. Central America and southern North America 115
5.4.1. Belize 115
5.4.2. Costa Rica 115
5.4.3. Honduras 118
5.4.4. Panama 118
5.4.5. Mexico 126
5.4.6. Central and southern Florida, USA 136
5.5. Caribbean Islands & Bermuda 140
5.5.1. Anguilla 140
5.5.2. Antigua 141
5.5.3. Aruba 143
5.5.4. Bahamas 143
5.5.5. Barbados 143
5.5.6. Bermuda 145
5.5.7. Bonaire 146
5.5.8. Cuba 146
5.5.9. Curaçao 149
5.5.10. Dominican Republic 150
5.5.11. The Grenadines 153
5.5.12. Haiti 154
5.5.13. Jamaica 155
5.5.14. Puerto Rico 164
5.5.15. Saint Barthélemy (St. Barts) 165
5.5.16. Saint Martin 166
5.5.17. Trinidad 166
5.6. Final Remarks 167
Chapter 6. The eye of the chimaera: Visual systems in fossil and extant podotreme crabs and their phylogenetic implications 186
6.1. Introduction 186
6.1.1. Basic eye types in crabs 186
6.1.2. Eyes types in larvae and post-larvae 187

  6.2. Materials and methods 189
    6.2.1. Materials.. 189
    6.2.2. Methods... 189
  6.3. Results... 190
    6.3.1. Eyes of †*Callichimaera perplexa*... 190
    6.3.2. Eyes of extant podotreme brachyurans 191
  6.4. Discussion 196
    6.4.1. Interpretation of ommatidial packing and facet shape in podotreme crabs........... 196
    6.4.2. The eye of the chimaera 198
    6.4.3. Eye preservation in fossil crabs... 199
    6.4.4. Phylogenetic implications 199
Chapter 7. Conclusions and prospects 214
  7.1. The fossil record of true crabs in the tropics.. 214
  7.2. Prospects and future directions 217
References.. 218
Appendix 1.. 249

List of Tables

Table 2.1. List of known taxa within †Telamonocarcinidae and †Tepexicarcinidae fam. nov. 30
Table 5.1. Geographic (left) and stratigraphic (right) distribution of 32 superfamilies and 69 families of anomurans and brachyurans with fossil records in tropical America summarized in this work.. ... 185
Table 6.1. List of extant podotreme and fossil brachyuran specimen studied bearing compound eyes... 212

List of Figures

Figure 1.1. Diversity of form across the main extant and fossil groups of true crabs. 8
Figure 1.2. Position of sexual openings in brachyuran crabs. 9
Figure 1.3. Selected phylogenetic hypotheses for Brachyura. 10
Figure 1.4. Types of compound eyes in brachyuran crabs. 11
Figure 2.1. A, locality map showing the approximate geographical provenance of †*Telamonocarcinus antiquus* sp. nov., holotype IGM p881012, near the town of La Fuente, Department of Santander, Colombia, South America.. 26
Figure 2.2. Oldest fossil Dorippidea from the Early and Late Cretaceous, family †Telamonocarcinidae. 27
Figure 2.4. Spatial and temporal ranges of the taxa currently included in †Telamonocarcinidae and †Tepexicarcinidae fam. nov................................ 29
Figure 3.1. Fossil Necrocarcinoidea preserving sternal features. 40
Figure 3.2. Fossil Necrocarcinoidea preserving sternal features (cont.). 41
Figure 3.3. General sternal configuration in †*Araripecarcinus* Martins–Neto, 1987, and representatives of the eight fossil and extant terminals of Raninomorpha. 42
Figure 3.4. Phylogenetic analyses excluding (I) and including (II) †*Araripecarcinus* Martins–Neto, 1987, respectively.. 43
Figure 3.5. Phylogenetic tree (A) and cladogram (B) showing the three main clades constituting the monophyletic Raninomorpha clade (white oval) 44
Figure 4.1. †*Callichimaera perplexa* n. gen. n. sp., lower Upper Cretaceous, Colombia. 64
Figure 4.2. †*Callichimaera perplexa* n. gen. n. sp, reconstruction.. 65
Figure 4.3. Phylogenetic relationships among the main families, superfamilies, and sections of 'true' crabs, or Brachyura. 66
Figure 4.4. Convergent decarcinized body forms in various families of anomuran and brachyuran crabs.. 67
Figure 5.1. Location map of the tropical and subtropical American countries, states, territories, or islands where fossil anomurans and brachyurans have been discovered/reported to date. 169
Figure 5.2. Schematic phylogenetic relationships among the superfamilies of Anomura and Brachyura listed in this work. 170
Figure 5.3**.** Fossil Anomura and Brachyura from the Cretaceous of Bolivia, South America 171
Figure 5.4**.** Fossil Brachyura from the Cretaceous and Neogene of Bolivia, South America. 172
Figure 5.5. Fossil Eubrachyura from the Cretaceous of Brazil, South America. 173
Figure 5.6. Fossil Eubrachyura from the Pleistocene of Brazil, South America. 174
Figure 5.7. Fossil Eubrachyura from the Cenozoic of Chile, South America. 175
Figure 5.8. Fossil Anomura and Brachyura from the Cretaceous and Cenozoic of Colombia, South America. 176
Figure 5.9. Fossil Eubrachyura from the Cenozoic of Peru, South America.. 177
Figure 5.10. Fossil Eubrachyura from the Cenozoic of Peru and Venezuela. 178
Figure 5.11. Fossil Anomura and Brachyura from Costa Rica and Panama, Central America. 179
Figure 5.12**.** Fossil Eubrachyura from Panama, Central America. 180
Figure 5.13. Fossil Anomura and Brachyura from Mexico 181
Figure 5.14. Fossil Anomura and Brachyura from southern central and central Florida. 182
Figure 5.15. Fossil Eubrachyura from southern and central Florida. 183
Figure 5.16. Fossil Anomura and Brachyura from the Neogene of the Caribbean. 184

Figure 6.1. Phylogenetic scenarios for the evolution of true crabs, and the distribution of their visual systems........ 201
Figure 6.2. Distribution of eye types in crabs across life stages. 202
Figure 6.3. Specimens of †*Callichimaera perplexa* with eyes preserved 203
Figure 6.4. Specimens of †*Callichimaera perplexa* with eyes preserved (cont.). 204
Figure 6.5. Homolodromioidea and Dromioidea. 205
Figure 6.6. Homoloidea. 206
Figure 6.7. Raninoidea. 207
Figure 6.8. Raninoidea (cont.). 208
Figure 6.9. Raninoidea and Cyclodorippoidea. 209
Figure 6.10. Other fossil brachyuran crabs preserving compound eyes. 210
Figure 6.11. Distribution of visual systems in Brachyura. 211

List of Abbreviations

Anatomical and phylogenetical abbreviations

A6: sixth pleonite

An: antennae

BI: Bayesian Inference

Ca: carpus

Cg: cervical groove

Ch: cheliped

C.I.: consistency index

Cx2–Cx4: coxa of second to fourth pereiopods

Cx Ch: coxa of cheliped

Cx mxp3: coxa of third maxillipeds

Da: dactylus

Ds: dorsal spine

E: compound eye

E4–E7: episternites four to seven

Ex mxp3: exopod of third maxillipeds

Le: left eye

Ma; millions of years ago

Me: merus

ML: Maximum Likelihood

MP: Maximum Parsimony

Mxp3: third maxillipeds

P2–P5: second to fifth pereiopods

Pr: propodus

R: rostrum

Re: right eye

Rs: rostral spine

R.I.: retention index

S3–S8: sternites three to eight

T.L.: treelength.

Institutional abbreviations

AMNH: American Museum of Natural History, New York, United States.

CIP: Centro de Investigaciones Palentológicas, Villa de Leyva, Boyacá, Colombia.

CPC: Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Coahuila, Mexico.

IGM: Colección Nacional de Paleontología, Instituto de Geología, UNAM, Mexico D.F., Mexico.

IGM p: Colecciones Paleontológicas Museo José Royo y Gómez, Servicio Geológico Colombiano, Bogotá D.C., Colombia

IHNFG: Colección Paleontológica de Chiapas, Museo Eliseo Palacios, Tuxtla Gutiérrez, Chiapas, Mexico.

LPURCA: Laboratório de Paleontologia da Universidade Regional do Cariri.

MFM: Mizunami Fossil Museum, Japan

MNHN: Muséum national d'Histoire naturelle, Paris, France.

MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro.

MSNMi: Museo Civico di Storia Naturale di Milano

MUN-STRI: Mapuka Museum of Universidad del Norte, Barranquilla, Colombia.

MUZ: Museo de Múzquiz, Múzquiz, Coahuila, Mexico.

NZGS: New Zealand Geological Survey, New Zealand.

QMW: Queensland Museum, Brisbane, Australia.

UF: Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA.

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

USP: Instituto de Geociències da Universidade São Paulo, São Paulo, Brazil.

Chapter 1. General introduction

A full understanding of the evolution of novel forms requires knowledge of their historical origins. This can be inferred via phylogenetic analyses of molecular and phenotypic variation in living forms, and clues from the fossil record. However, evolutionary origins of many groups are often obscure because a) few basal branches have living descendents, b) early fossils are rare and fragmentary, and often with unclear systematic affinities, and c) geographic centers of diversification are poorly known. This is the case for true crabs, or Brachyura, a diverse and economically important group whose evolutionary history and phylogenetic relationships remain unresolved. In addition, although regions like the tropics hold much of the world's modern biodiversity, and have been considered cradles and a museums of diversity through time (Jablonski *et al.*, 2006; Marshall, 2006), our knowledge of the fossil record from tropical regions is limited, largely due to enhanced tropical rock weathering, thick vegetation and ground cover, and a low number of scientists working in tropical paleontology. This general lack of knowledge of past diversity results in considerable biases when attempting to address major spatio-temporal and evolutionary questions such as: What role have mega-diverse areas like the Neotropics played in the evolution and diversification of crabs through time? Are phylogeny and ecology reliable predictors of distribution of convergent traits and across groups? How do extinct and extant branches in the crab tree of life relate to each other, and what can fossils tell us about the timing of origin of deep nodes?

True crabs, or Brachyura Latreille, 1802, are the most diverse and morphologically disparate of all decapods, with more than 7,000 extant species described (Ng *et al.*, 2008; Ahyong *et al.*, 2011; Tsang *et al.*, 2014), and over 3,000 more known from fossils (Schweitzer *et al.*, 2010; Luque *et al.*, 2017b). Curiously, brachyurans are also the youngest group of decapod crustaceans, first known from the early to mid Jurassic (~170–150 Ma) (Krobicki and Zatoń, 2008; Schweitzer and Feldmann, 2010c; Schweigert and Koppka, 2011), but they experienced major radiations worldwide during the Cretaceous (~145 to 66 Mya), with several lineages restricted to this time interval (Schweitzer and Feldmann, 2015) (Figure 1.1). In my thesis research I focused on the fossil record of crabs in the Neotropics, their systematic relationships with other fossil and extant crabs, and the diversity of their body forms and visual systems.

1.1. Systematic relationships among brachyuran crabs

Extant brachyurans can be roughly grouped into a handful of major body plans defined mainly by the shape of their carapace, claws, mouthparts, locomotory appendages, pleon, and the position of their sexual openings (Figure 1.2) (Guinot, 1977; Ng *et al.*, 2008; De Grave *et al.*, 2009; Karasawa *et al.*, 2011; Guinot *et al.*, 2013). These groups are the superfamilies Homolodromioidea Alcock, 1900a (Figure 1.1A) and Dromioidea De Haan, 1833, or 'sponge' crabs (Figure 1.1B); the Homoloidea De Haan, 1833, or 'carrier' crabs (Figure 1.1C); the Raninoidea De Haan, 1839, or 'frog' crabs (figure 1.1H); the Cyclodorippoidea Ortmann, 1892b (Figure 1.1J); and the section Eubrachyura Saint Laurent, 1980, known as the 'higher' true crabs, formed by several superfamilies placed in the subsections Heterotremata Guinot, 1977 (Figure 1.1.) and Thoracotremata Guinot, 1977 (Figure 1.1L). Molecular (e.g., Ahyong *et al.*, 2007; Tsang *et al.*, 2014), adult morphological (e.g., Ng *et al.*, 2008; Scholtz and McLay, 2009; Karasawa *et al.*, 2011), and spermatological studies (e.g., Jamieson *et al.*, 1995) (phylogenies based on larval morphology not available) agree that Brachyura is likely monophyletic and sister to false crabs and allies, collectively known as Anomura MacLeay, 1838 (Scholtz and Richter, 1995; Feldmann and Schweitzer, 2010b; Bracken-Grissom *et al.*, 2013). However, despite the supported monophyly of Brachyura, there is a lack of consensus on the organization of its higher taxa (Figure 1.3). Moreover, the systematic affinities of several fossil extinct groups such as Etyoidea Guinot and Tavares, 2001 (Figure 1.1E), Toryommoidea Glaessner, 1980 (Figure 1.1F), Dakoticancroidea Rathbun, 1917 (Figure 1.1I), and a novel chimaeric body plan (Figure 1.1D, see Chapter 4 of this thesis) remain unclear largely due to overall similarities with other brachyurans, thus obscuring their phylogenetic relationships with crown brachyurans through common descent.

Based primarily on the position of their sexual openings, Guinot (1977) grouped all the non–eubrachyuran taxa within a section Podotremata, characterized by the shared presence of the male and female sexual openings in the coxa of their walking legs (Figure 1.2A). This 'podotreme' condition differs from the 'sternitreme' condition seen in females of Eubrachyura (Heterotremata + Thoracotremata), where the sexual openings have migrated from a coxal to a sternal position (Figure 1.2B,C). Although Thoracotremata is largely regarded as a natural group, with both males and females having sternal sexual openings, whether ‘Heterotremata’ and ‘Podotremata’ are monophyletic remains contentious (Tavares, 2003) (Figure 1.3). If heterotreme crabs form a monophyletic clade sister to the thoracotremes, then their most recent shared common ancestor could not have been a heterotreme nor a thoracotreme. But if so, what were they? Alternatively, if the thoracotremes derived from a heterotreme ancestor, then ‘Heterotremata’ would not be a natural group but a grade with an already heterotreme common ancestor for crown Eubrachyura, and thus with some heterotreme lineages closer to the ancestor of Thoracotremata (Figure 1.3). Similarly, if ‘Podotremata’ is a natural group, then the most recent common ancestor of both Podotremata and Eubrachyura —collectively Brachyura — was neither a podotreme nor a sternitreme. Again, if so, what were they? A monophyletic Podotremata and a monophyletic Heterotremata rule out possible podotreme-to-heterotreme and heterotreme-to-thoracotreme scenarios.

Unraveling the systematic relationships across podotreme crabs is fundamental not only to understand the origins of Eubrachyura, but also the lower limits that define Brachyura itself, and thus its relations with Anomura (Tavares, 2003), the latter presenting the podotreme condition. Although molecular and morphological phylogenetics bring powerful tools to the study of relatedness at the genotypic and phenotypic levels, the fossil record provides a unique glimpse of the origins of such relatedness by revealing a past diversity otherwise unavailable. The spatial, temporal, and anatomical information provided by the fossil record is pivotal for model-based estimations of divergence rates by giving minimum ages for node calibrations, for understanding historical biogeography, and for assessing the polarity and direction of change of key traits leading to the forms seen today.

1.2. The roots of Eubrachyura

Among brachyurans, the diversity of species and anatomical disparity seen in the ‘higher’ crabs or Eubrachyura is matchless. They are the most widely distributed group of crabs, with species ranging from deep hydrothermal vents to reefs, rivers, caves, trees, and even as commensals of a range of invertebrates. Despite the extensive eubrachyuran fossil record from Late Cretaceous and Cenozoic rocks worldwide, occurrences during the Early Cretaceous are scarce and fragmentary, limiting our understanding on the origins of the group and their early morphological disparity. To date, only three families of eubrachyuran-like crabs are known from the Early Cretaceous: Componocancridae (Feldmann *et al.*, 2008a), and Tepexicarcinidae (Luque, 2015b; Chapter 2), both monospecific lineages from the lower Albian (~110–105 Mya) of North and Central America, respectively, and Priscinachidae Breton, 2009, from the upper Albian–Cenomanian (~105–95 Mya) of Spain (Klompmaker, 2013). The recent discovery of a new species of dorippoid eubrachyuran crab from the lower Albian of Colombia, South America (~113–110 Ma), increases the number of Early Cretaceous eubrachyuran-like families known worldwide (Chapter 2) to four, and provides new information on the earliest record of 'higher' true crabs from a moment of time where the group experienced its first documented major radiation.

1.3. The early origins of Raninoida

One of the most bewildering and puzzling groups of brachyurans is the Raninoidea, or 'frog crabs', whose unique anatomy has baffled scientists since Linnaean times. Our understanding of the evolution of raninoideans through time has changed dramatically during the last decades thanks to the discovery and re-studies of several key fossils, and the integration of information on fossil and extant taxa to test their phylogenetic relationships (Karasawa *et al.*, 2014; Luque, 2014a). The first account of the group is from Rumphus (1705), who illustrates the red spanner crab for the first time. In his Systema Naturae, Linnaeus (1758) named it *Cancer raninus* due to its resemblance to a frog (*Rana* means frog in Latin), but Lamarck (1801) recognized the uniqueness of this crab and assigned it to its own genus *Ranina*. Once considered to be primitive crabs due to their atypical non-crab-looking elongated bodies, narrow sterna, and a pleon that is partially exposed in dorsal view (Luque, 2015a; Chapter 3) their particular anatomy is known to reflect their infaunal back-burrowing lifestyle (van Bakel *et al.*, 2012a). But when did frog crabs start looking like frogs? Which are the closest extinct and extant relatives of crown raninoideans? What does the fossil record tell us about the polarity and direction of change of key raninoidean traits through time?

The evolutionary origin of frog crabs remains puzzling partly due to the astonishing morphological disparity seen in their fossil record, ranging from broad and heavily ornamented 'crab–like' taxa in the superfamily Necrocarcinoidea (Schweitzer *et al.*, 2016) (Figure 1.1D), to the elongate and smoother ‘frog–like’ modern Raninoidea (Figure 1.1H) (Tucker, 1998; Luque *et al.*, 2012; Karasawa *et al.*, 2014). However, an ancient Cretaceous superfamily, Palaeocorystoidea, displays both plesiomorphic and apomorphic traits that might advocate for either scenario; from ‘crab–like’ to ‘frog–like, or vice versa (Luque *et al.*, 2012; van Bakel *et al.*, 2012a). This lack of agreement is partly fuelled by the scarcity of Early Cretaceous fossils—the time period from when the first raninoidans are known. New fossil discoveries from the Cretaceous of northern South America (Chapters 3 and 5), together with re-examination of key museum specimens, reveal a previously unknown diversity of early stem raninoidans, push back the earliest records of several groups, and shed light on the origins and evolution of the group and their relatedness by common ancestry with extinct branches in the crab tree of life.

1.4. Novel forms in the fossil record

Modern phylogenomic techniques are becoming more powerful and affordable every day, permitting the study of rates and pathways of evolution of organisms and their likely relatedness through common descent in ways we could not have imagined a few decades ago. This has revolutionized our understanding of systematics and evolution, and undoubtedly will resolve several overarching questions in the decades to come. However, molecular approaches fail to predict the occurrence of extinct lineages and their morphological diversity, which can only be assessed directly from the fossil record. If it wasn’t for the geological record and the taphonomic processes that preserved the fossils it contains, we would have never been able to imagine the existence of organisms such as trilobites or eurypterids (sea scorpions), the iconic anomalocaridids from the Cambrian explosion of life, or even more iconic organisms such as non-avian dinosaurs. Without the clues from the fossil record, our understanding of the evolution of metazoan life through time would be severely limited.

Crabs are no exception. Their diversity today, albeit high, is just a brief snapshot of their geological history. In addition to the main podotreme groups living today, there are a number of extinct podotreme genera, families, and superfamilies distantly related to modern forms, and even groups so unusual that they may represent their own lineages in the crab tree of life, i.e., the Cretaceous Etyoidea (Figure 1.1E), Toryommoidea (Figure 1.1F), and Dakoticancroidea Figure 1.1I). The recent discovery of a new bizarre crab body plan from the Cretaceous of tropical America (Chapter 4), together with taxonomic and phylogenetic approaches, reveals a novel chimaeric body form that pushes the envelope for what a 'crab' is, and challenges conventional views of crab evolution by revealing repeated convergent loss of a typical 'crab-like' body form.

1.5. The fossil record of crabs in the tropical Americas

Our knowledge of fossil crustaceans from the tropics has increased considerably during the last decade, thanks to the discoveries of new fossils and the re-examination of museum specimens. However, several previous records have been misidentified, numerous museum specimens have never been reported, and many new discoveries are yet to be published. Shockingly, we know more about the fossil record of crabs from some small Caribbean islands like Jamaica than from much larger countries like Colombia, Perú, Ecuador and Bolivia all combined (Chapter 5). Evidence of this collecting bias motivated a thorough, detailed, up-to-date, and revised checklist for every marine, terrestrial, or freshwater fossil anomuran and brachyuran occurrence from tropical America, including the countries, islands, and territories from three main geographic regions: 1) northern South America (Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, and Venezuela); 2) Central and southern North America (Belize, Costa Rica, central and southern Florida, Honduras, Mexico, and Panama); and 3) the Caribbean Islands + Bermuda (Anguilla, Antigua, Aruba, Bahamas, Barbados, Bermuda, Bonaire, Cuba, Curaçao, Dominican Republic, The Grenadines, Haiti, Jamaica, Puerto Rico, Saint Bartélemy, Saint Martin, and Trinidad). The exceptional preservation of several of these fossils—some preserving details of the pleopods, mouthparts, antennae, and even their compound eyes—as well as their ages and geographic occurrences, provide the foundation for novel research in tropical fossil assemblages, their systematics, and historical biogeography.

1.6. Diversity of visual systems in crabs and their phylogenetic significance

Image-forming eyes are such a valuable adaptation that similar optical mechanisms have evolved independently in many higher taxa (Chapter 6). But if such complex organs have evolved independently multiple times, how useful are optical mechanisms for reconstructing phylogenetic relationships? Decapods in general, and crabs in particular, are ideal taxa to explore these questions because a) they have a good fossil record, b) they possess a great variety of optical designs, and c) details of eye form can be compared between living and fossil groups. Extant decapods exhibit four types of compound eyes: apposition, parabolic superposition, refracting superposition, and reflecting superposition (Land, 1976; Nilsson, 1988; Cronin and Porter, 2008). Each eye type has a distinctive external ommatidial arrangement and internal properties to focus light on the retina via different light paths (Gaten, 1998; Cronin and Porter, 2008). Interestingly, all four of these eye types occur in true crabs, or Brachyura, while most other crustacean taxa show only one type (Porter and Cronin, 2009).

As seen above, brachyuran crabs are usually divided into Podotremata and Eubrachyura based on the position of the female gonopores. Although Eubrachyura appears to be monophyletic, the monophyly of 'Podotremata' remains controversial. Early podotremes clades like Dromioidea, Homolodromioidea, and Homoloida have 'mirror' (reflecting superposition) eyes, which are plesiomorphic for Decapoda and found in several anomurans, lobsters, and most shrimps, while eubrachyurans have secondarily retained apposition eyes or evolved parabolic superposition types, but no 'mirror' eyes (Gaten, 1998; Porter and Cronin, 2009; Scholtz and McLay, 2009). Unfortunately, the optical mechanisms present in 'intermediate' podotremes are still poorly known, which motivated my investigation of the optical mechanisms present in fossil and extant podotremes. The study of museum specimens and new fossil material with eyes preserved (Chapter 6) have resulted in some preliminary observations regarding the distribution and evolution of visual systems.

1.7. Central questions addressed in this thesis

Several primary research questions motivated this dissertation research, mostly related to the evolution of novel form and functions through time. What are the roots of Eubrachyura, or 'higher' true crabs? How do podotreme brachyurans relate to each other, and in turn to Eubrachyura? What does the fossil record tell us about the polarity and direction of change of key traits leading to the particular 'frog-like' anatomy of modern Raninoidea and other decarcinized groups? Are phylogeny and ecology reliable predictors of the distribution of body forms and functions across taxa? Do visual systems provide clues about phylogenetic relationships among crab lineages?

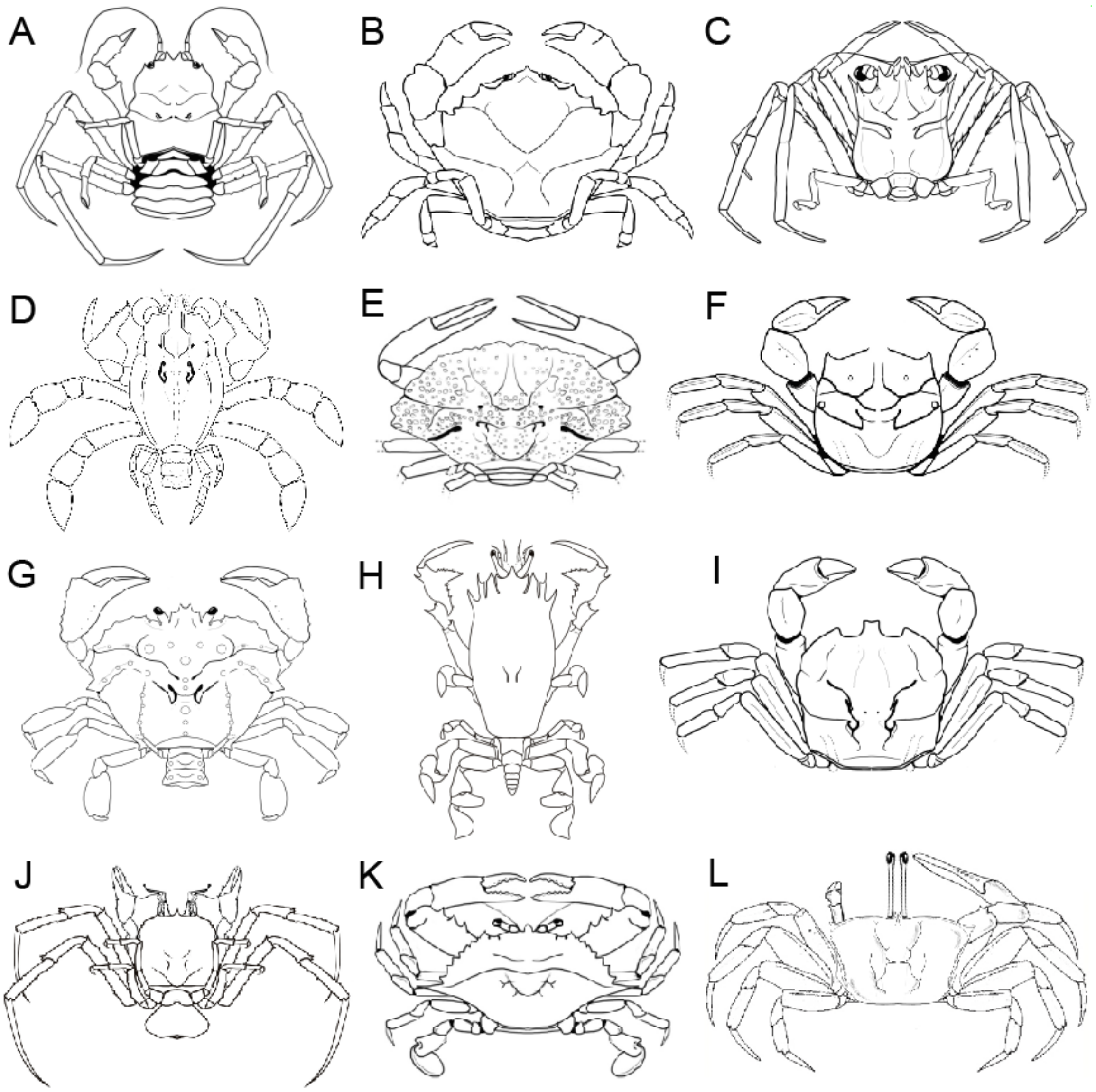


Figure 1.1. Diversity of form across the main extant and fossil groups of true crabs. A, Dromiacea: Homolodromioidea. B, Dromiacea: Dromioidea. C, Homoloidea. D, †Callichimeroidea. E, †Etyoida: †Etyoidea. F, †Torynommoidea. G. Raninoida: †Necrocarcinoidea. H, Raninoida: Raninoidea. I, †Dakoticancroidea. J. Cyclodorippoidea. K, Eubrachyura: Heterotremata. L, Eubrachyura: Thoracotremata. Dagger (†) indicates extinct groups. Line drawings not to scale.

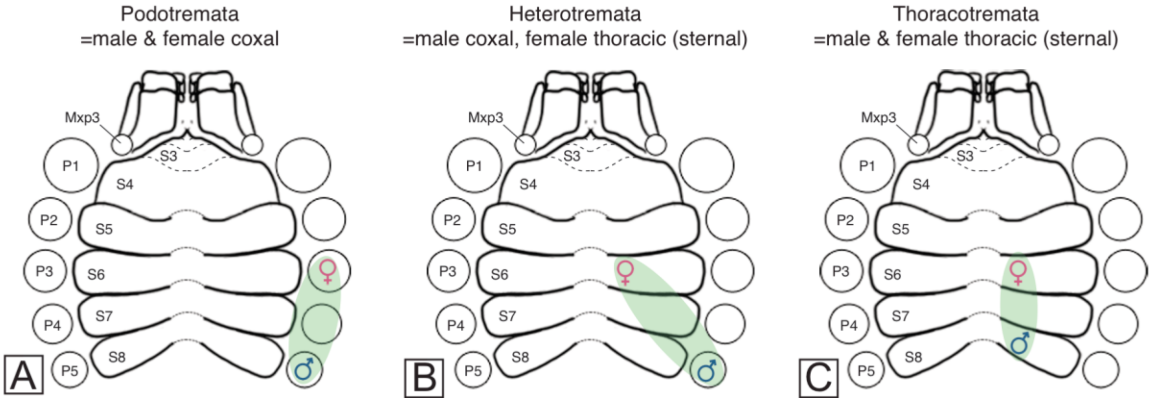


Figure 1.2. Position of sexual openings in brachyuran crabs. A, podotreme condition; B, heterotreme condition; C, thoracotreme condition. For all decapods, including Anomura and Brachyura, the plesiomorphic condition is males and females with coxal sexual openings, or podotreme. The innovation of sternal sexual openings in female crabs is presumed to have occurred once in the most recent common ancestor for heterotreme and thoracotreme crabs (=Eubrachyura).

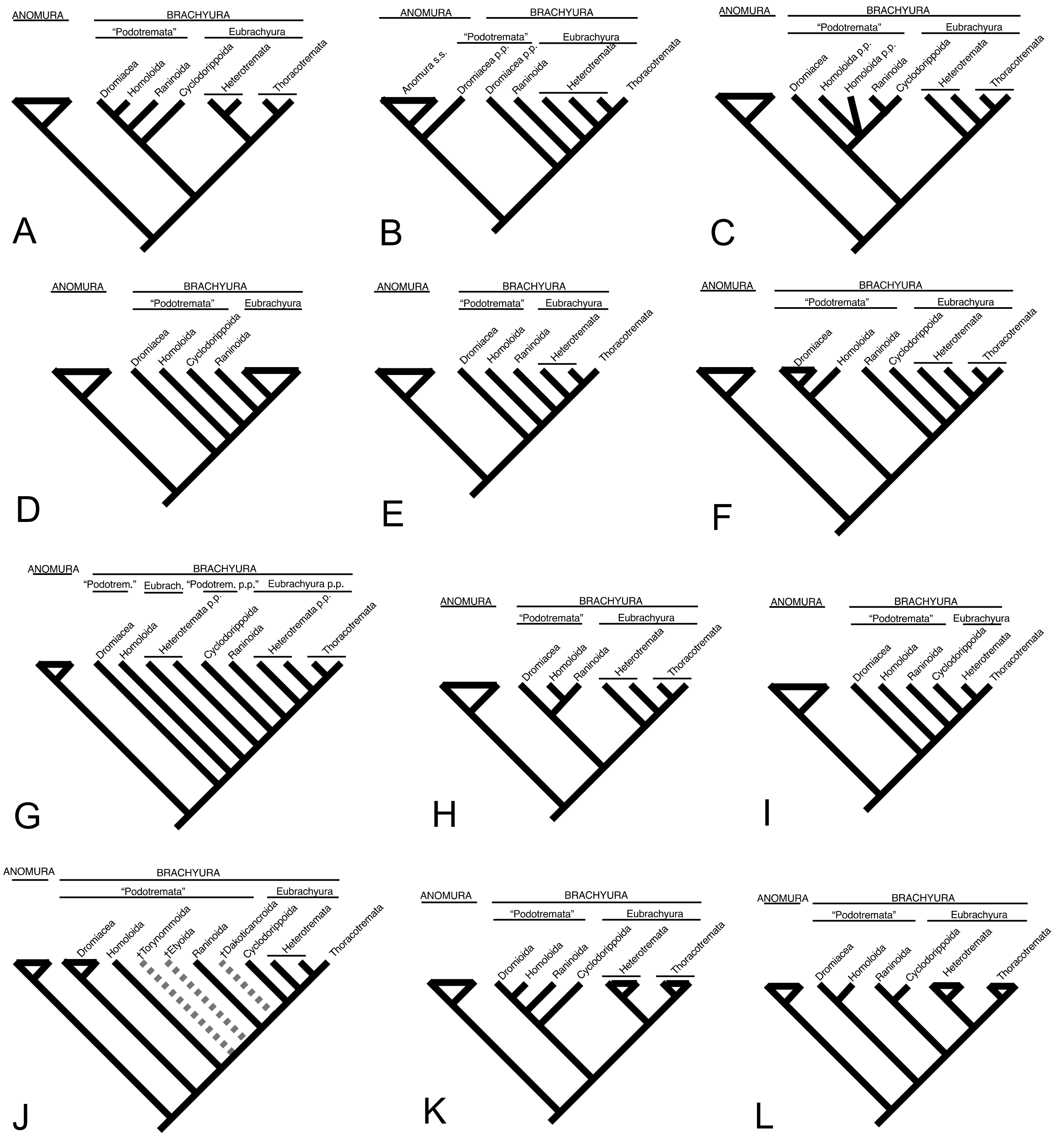


Figure 1.3. Selected phylogenetic hypotheses for Brachyura. Note that Anomura is usually included in the outgroup as reciprocal sister clade to Brachyura. A: after Guinot (1977), based on the position of sexual openings in males and females (hand reconstruction). B: after Spears et al. (1992, fig. 3), based on 18S rRNA. C: after Jamieson et al. (1995), based on spermatozoal ultrastructure. D: after McLay (1999) (modified after Ahyong *et al.*, 2007, fig. 1b). E: after Ahyong and O'Meally (2004, fig. 3), based on 16S, 18S, and 28S rRNA. F: after Ahyong et al. (2007, fig. 4), based on 18S rRNA. G: after Brösing et al. (2007, fig. 3), based on foregut characters. H: after Tsang et al. (2008, fig. 2), based on two nuclear protein–coding genes (phosphoenolpyruvate carboxykinase and sodium–potassium ATPase a–subunit). I: Scholtz and McLay (2009, fig. 3), based on morphological characters of extant brachyurans (hand reconstruction). J: after Karasawa et al. (2011, fig. 3), maximum parsimony based on adult morphological data of fossil and extant taxa. K: after Guinot et al. (2013), based on morphological data (hand reconstruction). L: after Tsang et al. (2014, fig. 1), based on 12S, 16S, AK, Enolase, GAPDH, H3, NaK, PepCK.

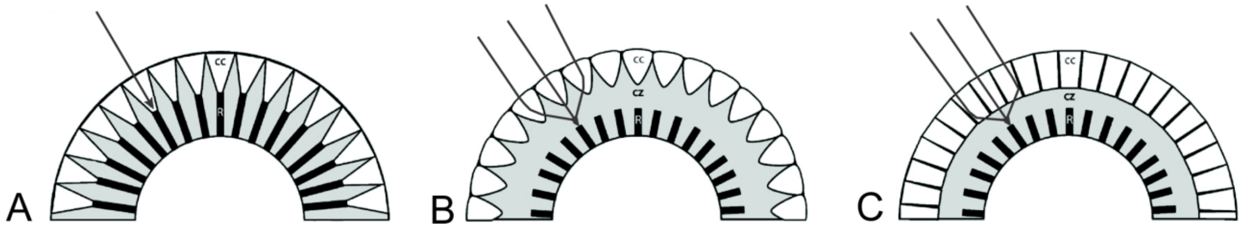


Figure 1.4. Types of compound eyes in brachyuran crabs. A: Apposition eye = evolved for vision in relatively bright light. A single light beam is focused on the retina of a single ommatidium (dashed line). B–C: superposition eyes = better suited for vision in dim light. Recognized by the presence of a “clear zone” between the outer structures of the eye and the retina (grey area). B: refracting superposition = the crystalline cones contain a refractive index gradient that bend incoming light to focus it on the retina (dashed lines); multiple beams of light may fall on a single ommatidial retina. C: reflecting superposition = focus an image by reflections off the sides of the cones, which are square instead of round in cross section, and are typical of ‘mirror’ optics; heret too, multiple beams of light may fall on a single ommatidial retina. Abbreviations: cc=crystalline cone; cz=clear zone; r=rhabdom. Drawings modified from Cronin and Porter (2008). Parabolic superposition not illustrated..

Chapter 2. The oldest ‘higher’ true crabs (Crustacea: Decapoda: Brachyura): Insights from the Early Cretaceous of the Americas

2.1. Introduction

True crabs (Brachyura) are the most derived clade of decapod crustaceans, and exhibit an astonishing diversity of body plans not seen among other decapods. The most debatable trait for grouping brachyurans is the position of the female’s sexual openings; either at the base of the legs (=podotremes), or at the thoracic sternum (=eubrachyurans) (Guinot, 1977; Saint Laurent, 1980; Guinot and Quenette, 2005; Guinot *et al.*, 2013). Although the monophyly of podotremes is still debated, there is a general consensus that Eubrachyura, or ‘higher’ true crabs, is a monophyletic clade (Spears *et al.*, 1992; Ahyong *et al.*, 2007; Brösing *et al.*, 2007; Ng *et al.*, 2008; Scholtz and McLay, 2009, Karasawa *et al.*, 2011, Tsang *et al.*, 2014, among others). However, while fossil eubrachyurans are relatively well known from Late Cretaceous and Cenozoic deposits worldwide, little is known about their Early Cretaceous history, obscuring our understanding on their early disparity. Documenting the fossil record of Brachyura is crucial to our comprehension of the relationships among the main extant crab lineages. This is because all the diversity seen today is the result of millions of years of evolution; thus, modern body plans are derived lineages descending from early branches in the brachyuran evolutionary tree. In addition, many distinctive body plans are restricted to the Cretaceous; a time when Brachyura flourished and diversified. These groups provide unique information about the relatedness by common ancestry of extant clades, and the polarity of changes in diagnostic traits that unite today’s main body plans. To date, the only known Early Cretaceous eubrachyuran families are Componocancridae Feldmann, Schweitzer and Green, 2008a, and Tepexicarcinidae fam. nov., both from the Albian of North and Central America (~110–100 Ma). Herein I report a new species of early eubrachyuran, †*Telamonocarcinus antiquus* sp. nov., from the Early Albian of Colombia, South America (~115 Ma), and discuss its spatial and temporal implications for the origins of higher true crabs.

2.2. Geological setting

†*Telamonocarcinus antiquus* sp. nov. was discovered in black–greyish, terrigenous, gypsum-rich, micaceous shales of the lowermost Tablazo Formation, cropping out near the contact with the underlying Paja Formation in a small quarry, approximately 30 meters from El Salitre Creek, countryside of El Batán, Montegrande, near the town of La Fuente, Department of Santander, Colombian Eastern Cordillera; Latitude N 06°43′30″, Longitude W 73°15′32″ (Fig. 2.1A). The Tablazo Formation was described by Wheeler (in Morales *et al.*, 1958) as a succession constituted principally of thick fossiliferous limestone in the upper portion, and calcareous mudstones with arenitic intervals in the lower portion, cropping out in the area known as El Tablazo, where the main road from Bucaramanga to San Vicente de Chucurí intersects the Sogamoso River, approximately 36 km north–northwest from where †*Telamonocarcinus antiquus* sp. nov. was discovered. In the area, the unit overlies the gray fossiliferous shales and limestones with concretionary levels of the Paja Formation (Barremian–upper Aptian), and underlies the predominant light to dark mudstones interspersed with sporadic sandstones of the Simití Formation (middle–upper Albian) (Morales *et al.*, 1958; Julivert, 1968; Pulido, 1985; Moreno and Sarmiento, 2002) (Fig. 2.1B). Morales *et al.* (1958) reported from the Tablazo Formation the ammonite genera *Uhligella* Jacob, 1907*, Cheloniceras* Hyatt, 1903, *Parahoplites* Anthula, 1899*,* and stratigraphically above, the genus *Douvilleiceras* Grossouvre, 1894, indicating a Late Aptian–Early Albian age (Julivert, 1968; Moreno and Sarmiento, 2002). The area of study is structurally complex, with several faults dislocating blocks associated with the trace of the Suarez fault (Pulido, 1979, 1985) (Fig. 2.1B). In addition, the region is densely vegetated, resulting in poor exposure of outcrops that are mainly restricted to some road cuts. Despite this, recent field explorations resulted in the discovery of several decapod crustacean remains at the base of the Tablazo Formation near the contact with the Paja Formation, associated to ammonite fragments of *Neodeshayesites* sp. indet. which correspond to the *Douvilleiceras solitae–Neodeshayesites columbianus* zone (Etayo-Serna, 1979, p. 14), thus indicating an Early Albian age for the rocks containing †*Telamonocarcinus antiquus* sp. nov. (Etayo-Serna, Terraza, and Montoya pers. comm., September 2014).

The Paja Formation is one of the most prolific and vastly studied fossiliferous units in Colombia, which has yielded an impressive array of plants (e.g. Huertas, 1967, 1970, 1976; van Waveren *et* *al.*, 2002), marine vertebrates including fishes and reptiles (e.g. Acosta *et al.*, 1979; Hampe, 1992; Schultze and Stöhr, 1996; Páramo, 1997; 2005), invertebrates such as ammonites and bivalves (e.g. Etayo-Serna, 1968b, 1968a, 1979; Villamil, 1998; Patarroyo, 2000; Hoedemaeker, 2004; among many others), and most recently decapod crustaceans such as the homoloid crab †*Mithracites takedai* Van Bakel, Guinot, Jagt, and Fraaije, 2012b, the raninoidans †*Planocarcinus olssoni* (Rathbun, 1937), †*Joeranina kerri* (Luque, Feldmann, Schweitzer, Jaramillo, and Cameron, 2012), †*Colombicarcinus laevis* Karasawa, Schweitzer, Feldmann, and Luque, 2014, †*Bellcarcinus aptiensis* Luque, 2014b, and other podotreme crabs (Cortés and Luque, unpublished). However, little is known about the paleontological content of the Tablazo Formation, and no fossil crustaceans from this unit have been reported to date. The discovery of †*Telamonocarcinus antiquus* sp. nov. (Fig. 2.2A), in association with callianassid shrimps, mecochirid lobsters, and palaeocorystid crabs (Fig. 2.3), represents the first record of marine arthropods known from the Tablazo Formation, and provides valuable information for more detailed palaeoecological reconstructions of these shallow marine settings during Late Cretaceous times.

2.3. Material and methods

The holotype and sole specimen of †*Telamonocarcinus antiquus* sp. nov. under acronym and catalogue number IGM p881012, was collected in May, 2012, and is deposited in the paleontological collections of the Colombian Geological Survey, Bogotá, Colombia. The specimen was coated with sublimated ammonium chloride prior of photography to enhance relief of dorsal grooves, regions, and fine tubercles, and photographed under a Leica Macroscope with Spotflex digital camera. The resulting multilayered stack of photos were merged into a single high–definition image using the stacking software Helicon Focus Pro 6.2.2.

2.4. Results

2.4.1. Systematic palaeontology

This published work and the nomenclatural acts it contains, have been registered in Zoobank: http://zoobank.org/References/996C0842-8077-4F4A-AD55-A71FC0171A0C.

Infraorder **Brachyura** Latreille, 1802

Section **Eubrachyura** Saint Laurent, 1980

Superfamily **Dorippoidea** MacLeay, 1838

Family †**Telamonocarcinidae** Larghi, 2004

Figure 2.2

Included genera. †*Eodorippe* Glaessner, 1980; †*Telamonocarcinus* Larghi, 2004 (type genus).

Emended Diagnosis. Dorsal carapace nearly as wide as long (†*Eodorippe*) or wider (†*Telamonocarcinus*), broadly pyriform in outline; carapace maximum width at about posterior third of carapace, at level of branchial regions. Fronto-orbital margin broad, slightly more than half carapace width; rostrum long, narrow, subtriangular, broader at the base; orbits wide, lacking orbital fissures and spines; eyes large, with long eyestalks in †*Telamonocarcinus*, unknown for *Eodorippe*; outer-orbital spine produced and diverging anterolaterally (†*Telamonocarcinus*) or less produced and converging antero–mesially (†*Eodorippe*). Anterolateral margin short, lacking spines posterior to outer orbital spine; posterolateral margin poorly defined, longer than anterolateral margin, broad, rounded; posterior margin shorter than fronto–orbital margin, about one–third carapace width, slightly concave, rimmed. Cervical and branchial grooves distinct, reaching anterolateral margin, subparallel, close to one other, delimiting a narrow epibranchial region. Dorsal carapace moderately to coarsely granulate; carapace regions well delimited by grooves. Chelipeds nearly isochelous (†*Telamonocarcinus*, unknown for †*Eodorippe*). Pereiopods 2 to 3 the longest, very similar in shape, with P3 slightly longer than P2; pereiopods 4 to 5 reduced, without a subchelate dactyl (†*Telamonocarcinus*, unknown for †*Eodorippe*). Thoracic sternum subpentagonal, with large sternites 5 and 6; sternal sutures 4/5–6/7 incomplete, only known for †*Telamonocarcinus.* Male pleon with six somites and telson; first 3 pleonites dorsally exposed (†*Telamonocarcinus*, unknown for †*Eodorippe*).

Absence of female gonopores on coxa of third pereiopod (†*Telamonocarcinus*) (after Larghi, 2004, p. 535, and Guinot *et al.*, 2013, p. 306).

Stratigraphic range. Lower Cretaceous (Aptian) to Upper Cretaceous (Campanian–Maastrichtian) (Fig. 2.4, Table 2.1).

Taxonomic remarks. The fossil record of †Telamonocarcinidae is sparse and fragmentary, with three out of the four known species represented only by the dorsal carapace of their holotypes. The lack of preserved thoracic sternum, pleon, or appendages in both species of †*Eodorippe* and in †*Telamonocarcinus antiquus* sp. nov., precludes detailed discussion of their phylogenetic affinities with other brachyurans. Based on the carapace outline, Glaessner (1980) and Collins *et al.* (1993) included †*Eodorippe* within the podotreme †Torynommidae Glaessner, 1980, and highlighted their resemblance to Dorippidae, a family purported as one of the most basal eubrachyuran clades. †*Telamonocarcinus gambalatus* Larghi, 2004, is the only telamonocarcinid species known from dorsal and ventral specimens, and its distinctive carapace outline, dorsal regions, groove patterns, orbital configuration and the females apparently lacking gonopores in the coxa of P3, led Larghi (2004) to conclude that the subfamily †Telamonocarcininae might be closer to the eubrachyuran Dorippidae than to the podotreme †Torynommoidea or Cyclodorippoidea. This subfamily was recently elevated to full family status by Guinot *et al.* (2013), and alongside Dorippidae, Ethusidae, and †Goniochelidae Schweitzer and Feldmann, 2011b, constitute the superfamily Dorippoidea (Glaessner, 1969; Castro, 2005; Guinot *et al.*, 2008; Ng *et al.*, 2008; Schweitzer and Feldmann, 2011b). A detailed discussion of the dorippoid affinities of †Telamonocarcinidae was provided by Guinot *et al.*, (2013), who stated that its mixture of dorippid and ethusid traits might indicate that the family is not monophyletic. I concur. †*Telamonocarcinus* and †*Eodorippe* have a combination of dorsal traits that can be seen in either Dorippidae or Ethusidae. Larghi, (2004) and Guinot *et al.*, (2013) commented on the similarities and differences between the two telamonocarcinid genera. Among the most conspicuous differences is the configuration of the fronto-orbital margin. In †*Telamonocarcinus*, the outer-orbital spine is produced and directed anterolaterally, whereas in †*Eodorippe* it is reduced and converges antero-mesially. Similar variation in shape, size, and orientation of the outer-orbital spines can also be seen among dorippids and ethusids. Although the rostrum is poorly known in †*Telamonocarcinus*, in †*Eodorippe* it seems to be subtriangular, long, and narrow. Unfortunately, based solely on the illustrated ventral females of †*T. gambalatus* in Larghi (2004), I cannot conclude if the position of the gonopores is sternal or coxal, warranting placement of †*Telamonocarcinus* and †*Eodorippe* within Eubrachyura, and particularly with Dorippidae or Ethusidae. On the other hand, based on the morphology of †*Telamonocarcinus* and †*Eodorippe* dorsal carapaces, they appear to be closer to the dorippoidean body plan than to any other brachyuran. †Telamonocarcinidae shares superficial similarities in carapace shape and dorsal features with some taxa within †Retroplumoidea Gill, 1894, but differs considerably on the narrower, non-bilobate rostrum, the frontoorbital configuration, and having both P4–P5 reduced, while in retroplumoids only P5 is reduced. †Telamonocarcinidae shares with †Torynommoidea the reduced P4–P5, but the latter differs on its wider orbits with a short intraorbital spine, the rostral configuration, the less inflated branchial regions, the subquadrate carapace with nearly parallel lateral margins, and the subparallel cervical and branchiocardiac grooves (Schweitzer and Feldmann, 2011a; Karasawa *et al.*, 2014). Due the nature of the information available on telamonocarcinid taxa, affiliation with Dorippoidea seems to be the most supported hypothesis.

A taxon that has been previously included within †Telamonocarcinidae is †*Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate, and Bishop, 1998b (Larghi, 2004; Guinot *et al.*, 2008). However, based on the work of Guinot *et al.* (2013), and following the original descriptions and illustrations by Feldmann *et al.* (1998b)(1998) and Vega *et al.*, (2005), †*Tepexicarcinus* appears to be distinctive dorsally and ventrally enough from †Telamonocarcinidae, Ethusidae or Dorippidae, that it may represent its own evolutionary lineage of early eubrachyuran or stem-eubrachyuran crabs. Therefore, †*Tepexicarcinus* warrants independent suprageneric placement, as discussed below.

Genus †***Eodorippe*** Glaessner, 1980

Figure 2.2E–F

Type species. †*Eodorippe spedeni* Glaessner, 1980, by original designation.

Other species. †*Eodorippe binodosus* Collins, Kanie, and Karasawa, 1993.

Emended Diagnosis. Dorsal carapace nearly as wide as long or slightly wider; with maximum width at posterior third of carapace. Fronto-orbital margin broad, with orbits lacking spines or fissures; rostrum subtriangular, short (†*E. binodosus*), or long (†*E. spedeni*), broader at its base. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region not flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately to faintly granulated.

Stratigraphic range. Upper Cretaceous (Cenomanian to ?Maastrichtian) (Fig. 2.4, Table 2.1).

Taxonomic remarks. *Eodorippe spedeni* differs from †*Telamonocarcinus gambalatus* and *T. antiquus* sp. nov. in the degree of development of the outer orbital spine, that is more produced and diverging anterolaterally in †*Telamonocarcinus*, but less produced and converging antero-mesially in *E. spedeni* (Fig. 2.2, arrows). †*Eodorippe binodosus* was considered to be congeneric with †*Telamonocarcinus* by Larghi (2004), and Guinot *et al.* (2013). In my view, the presence of short and converging outer orbital spines in †*E. binodosus*, and the lack of the narrow and subparallel lobes flanking the cardiac region differ from †*Telamonocarcinus* spp., suggesting affinity with †*Eodorippe*, as originally envisioned by Collins *et al.* (1993). Discovery of ventral material will allow testing of its generic placement.

Genus †***Telamonocarcinus*** Larghi, 2004

Figure 2.2A–D

Type species. †*Telamonocarcinus gambalatus* Larghi, 2004, by original designation.

Other species. †*Telamonocarcinus antiquus* sp. nov.

Emended Diagnosis. Crabs with carapace wider than long, broadly pyriform in outline, with maximum width at posterior third of carapace; anterolateral margin poorly defined, short, lacking teeth; posterolateral margin poorly defined, longer than anterolateral margin, broad, rounded; posterior margin short, about one–third carapace width, weakly concave, rimmed; fronto–orbital margin broad, with orbits lacking spines or fissures; rostrum long and narrow, subtriangular, broader at its base. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately to coarsely granulated. Absence of female gonopores on coxa of third pereiopod. Male pleon with six somites and telson.

Stratigraphic range. Lower Cretaceous (Aptian) to Upper Cretaceous (Cenomanian) (Fig. 2.4, Table 2.1).

Taxonomic remarks. In addition to the more produced and anterolaterally diverging outer–orbital spine, *Telamonocarcinus* also differs from †*Eodorippe spedeni* and †*E. binodosus* in the possession of subparallel narrow lobes flanking laterally the cardiac region (Fig. 2.2). Given the low species richness of †Telamonocarcinidae, it is hard to tell whether these traits represent the plesiomorphic or apomorphic conditions for the clade.

Schweitzer *et al.* (2003b) described an indeterminate genus and species of brachyuran crab from the Cenomanian of Egypt, which was considered by Garassino *et al.* (2008, p. 61) as conspecific with †*Telamonocarcinus gambalatus.* Unfortunately, the taxon is poorly preserved, and not much can be concluded regarding its systematic affinities. Nevertheless, it must be noted that a specimen illustrated by Schweitzer *et al.* (2003b, fig. 1.1) lacks the diagnostic wider than long pyriform carapace, indicating that the taxon is not conspecific with †*T. gambalatus*, nor is it congeneric with †*Telamonocarcinus.* In fact, its apparently longer-than-wide carapace with long and nearly straight posterolateral margins aligns it more closely to †Tepexicarcinidae fam. nov., to which the enigmatic taxon is herein assigned until better material becomes available for study.

†***Telamonocarcinus antiquus*** sp. nov.

LSID. urn:lsid:zoobank.org:act:BDC32DC8-3327-4E1D-B94B-6D620D255310

Figure 2.2A

Etymology. From the Latin word for ‘ancient, old’, alluding to its age with respect to the oldest records of telamonocarcinid, dorippoidean, and eubrachyuran crabs.

Diagnosis. Carapace wider than long, broadly pyriform in outline, with maximum width at posterior third of carapace; anterolateral margin poorly defined, short, lacking teeth; posterolateral margin poorly defined, broad, rounded; posterior margin short, slightly concave, rimmed; fronto-orbital margin poorly preserved, apparently wide, with orbits lacking spines or fissures. Cervical and branchiocardiac grooves distinct, as are carapace regions; cardiac region flanked laterally by two subparallel narrow lobes. Dorsal carapace moderately granulated.

Description. Carapace pyriform in outline, wider than long, maximum width at posterior third; fronto-orbital margin poorly preserved in the holotype, apparently wide, about 60% as wide as carapace maximum width; anterolateral margin distinct, short, weakly convex, lacking spines; posterolateral margin distinct, about twice as long as anterolateral margin, strongly convex, lacking spines; posterior margin sinuous, rimmed dorsally, concave at mid portion, and convex toward posterolateral margin. Cervical groove distinct, well developed, slightly interrupted axially, reaching anterolateral margin of carapace; branchial groove distinct, well developed, deep, flanking the metagastric region; branchiocardiac groove distinct, well developed, reaching anterolateral margin of carapace, subparallel to cervical groove, bounding a very narrow epibranchial region. Epigastric region distinct, narrow, wider than long, extending from base of rostrum to mesogastric region, axially ridged and delimited by two parallel ridges; protogastric region distinct, wide, separated mesially by mesogastric region, bearing one tubercle; hepatic region distinct, small, subtriangular, bearing a central tubercle; mesogastric region distinct, wider than long, bearing a small medial tubercle; metagastric region small, wider than long, subtrapezoidal, lying posterior to mesogastric region and separated by axial portion of cervical groove, flanked laterally by branchial groove, and posteriorly depressed at boundary with urogastric region; urogastric region small, subrectangular; cardiac region about as long as wide, wider anteriorly at contact with urogastric region, narrowing posteriorly, flanked laterally by two subparallel narrow lobes, separating the cardiac region from the branchial regions; intestinal region wide, narrower axially near contact with cardiac region. Epibranchial region distinct, well developed, narrow, extending anterodistally from branchial region, delimited anteriorly by cervical groove, and posteriorly by branchiocardiac groove; branchial regions well developed.

Anterior carapace regions well defined; epigastric region ridged axially, delimited by lateral, nearly parallel grooves; protogastric and hepatic regions bearing one tubercle; mesogastric region subpentagonal in outline, narrower anteriorly, rapidly broadening posteriorly, bearing one tubercle anterior to axial portion of cervical groove; metagastric region distinct, subtrapezoidal, wider anteriorly, about as wide as mesogastric region, narrower posteriorly, bounded laterally by branchial grooves; cardiac region well defined, narrow anteriorly, separated from metagastric region by a shallow groove, wider posteriorly, separated from cardiac region by a short, transverse ridge; cardiac region subtriangular, wider anteriorly, narrowing posteriorly, bearing one posterior swollen node, laterally delimited by short, deep longitudinal furrows, flanking two lateral, subparallel narrow lobes; intestinal region wide.

Measurements. Carapace maximum length: ~ 4.7 mm, measured from posterior margin to the base of rostrum; carapace maximum width: ~6.5 mm; fronto–orbital margin estimated width: ~3.6 mm.

Stratigraphic range. Lower Cretaceous (lower Albian) (Fig. 2.4, Table 2.1).

Remarks. †*Telamonocarcinus antiquus* sp. nov. is assigned to †*Telamonocarcinus* based on its carapace outline, the dorsal groove patterns, the well developed epigastric and mesogastric regions, and the small subparallel swellings flanking the cardiac region. This taxon noticeably differs from †*T. gambalatus*, the only other described species in the genus, in the size and density of the dorsal granules, being coarser in the latter. Unfortunately, the holotype and sole specimen of †*T. antiquus* sp. nov. has a poorly preserved fronto–orbital margin, and no thoracic sternum, appendages, or pleon was recovered, precluding a more detailed comparison with †*T. gambalatus* or other taxa within †Telamonocarcinidae at this time, or to confirm sex or growth stage.

Superfamily uncertain

†**Tepexicarcinidae** fam. nov.

LSID. urn:lsid:zoobank.org:act:AC082EBE-3C94-4F7E-B511-C10626ED40F4

Included genera. †*Tepexicarcinus* Feldmann, Vega, Applegate, and Bishop, 1998b, by original designation; tentatively genus and species indeterminate *in* Schweitzer *et al.*, 2003b, p. 890, figs. 1–2.

Diagnosis. Carapace longer than wide, with subrectangular outline; carapace maximum width positioned at anterior third of carapace. Fronto-orbital margin wide, about 70% carapace width; rostrum square, conspicuously bifid, broader at the tip, sulcate axially; orbits semi-circular, short, bearing two orbital fissures; outer orbital spine short, directed forward; anterolateral margin short, slightly convex, bearing three spines. Lateral margins long, straight, nearly parallel; posterior margin about 75% carapace width, almost straight, slightly convex axially, nearly as wide as fronto–orbital margin. Dorsal carapace finely punctate. Cervical and branchiocardiac grooves distinct, reaching lateral margins, nearly parallel but distant from each other, bounding a broad epibranchial region. Epibranchial region wide, comprising about the

33% of dorsal carapace, bounded by cervical and branchiocardiac grooves. Chelipeds subequal. Pereiopods 2 to 3 the longest, similar in shape, with P3 larger than P2; Pereiopods 4 to 5 shorter; P5 shortest, and carried subdorsally. Thoracic sternum subpentagonal, with large sternites 5 and 6. Pleon with four free somites and two fused, plus telson (after Feldmann *et al.*, 1998b, pp. 86–87, fig. 7; and Vega *et al.*, 2005, pp. 28–29, fig. 4, pl. 2; and following Larghi, 2004, and Guinot *et al.*, 2013).

Taxonomic remarks. The distinctive set of diagnostic traits of †*Tepexicarcinus* is unique among †Telamonocarcinidae, Dorippidae and even Ethusidae, meriting its elevation to family rank. In fact, †Tepexicarcinidae fam. nov. might actually represent an independent evolutionary lineage of early eubrachyurans, and probably should be better placed in its own superfamily †Tepexicarcinoidea, since no other brachyuran superfamily matches its body plan. †*Tepexicarcinus* shares with some dorippoids the long pereiopods 2–3 with large dactyli (Schweitzer and Feldmann, 2011b), and particularly with extant Ethusidae males the possession of a pleon constituted by free and fused somites, unlike †*Telamonocarcinus* and extant Dorippidae that have six free somites (Larghi, 2004; Guinot *et al.* 2013), but these traits do not warrant affiliation with Dorippoidea. Future specimens preserving additional dorsal and ventral features will allow detailed comparisons with other 'basal' fossil and extant eubrachyurans.

Genus †*Tepexicarcinus* Feldmann, Vega, Applegate, and Bishop, 1998b

Included species. †*Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate, and Bishop, 1998b, by original designation.

Stratigraphic range. Lower Cretaceous (Albian) (Fig. 2.4, Table 2.1).

Taxonomic remarks. †*Tepexicarcinus tlayuaensis*, the sole genus and species within †Tepexicarcinidae fam. nov., was described and illustrated in detail by Feldmann *et al.* (1998b) (1998) and Vega *et al.* (2005). The specimen designated genus and species indeterminate of Schweitzer *et al.* (2003b) shares with †*Tepexicarcinus* the longer than wide carapace with long and nearly straight posterolateral margins, but differs from the latter in its noticeably shorter P2 with respect to P3, its P3 merus is slightly curved backwards and is wider at the junction with the carpus, and its P3 dactyl is longer than the propodus and the merus. The two taxa seem not to be congeneric, and provisional placement of the genus and species indeterminate of Schweitzer *et al.* (2003b) within †Tepexicarcininae should be reconsidered in the light of new material, when it becomes available.

2.5. Discussion

Besides †*Telamonocarcinus antiquus* sp. nov. from the Aptian Paja Formation of Colombia, and †*Tepexicarcinus tlayuaensis* from the Albian Tlayúa Formation of Mexico (Table 2.1), the only other Early Cretaceous eubrachyuran-like crab known is †*Componocancer roberti* Feldmann, Schweitzer, and Green, 2008a, from the Albian Shell Creek Shale of Montana, USA. †*Componocancer roberti*, the sole species within the superfamily †Componocancroidea, displays a combination of brachyuran plesiomorphies (e.g., laterally unfused thoracic sternites, posterior thoracic sternites and their associated legs reduced and directed postero-dorsally) and eubrachyuran synapomorphies (i.e., a large vulva on female's sixth thoracic sternites) that set it apart from other early–branching eubrachyuran clades. The Albian crab †*Hillius youngi* Bishop, 1983b, was once considered as a possible eubrachyuran with dorippoid affinities (Bishop, 1983b; De Grave *et al.*, 2009; Schweitzer *et al.*, 2010), but recent works documented *Hillius* as a podotreme, either related to cyclodorippoidans, particularly with Cyclodorippidae Ortmann, 1892b (Karasawa *et al.*, 2011; Schweitzer and Feldmann, 2011b), or raninoidans, particularly with †Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg, and Ross, 2003a (van Bakel *et al.*, 2012a; Guinot *et al.* 2013).

†*Telamonocarcinus* ranged from the south-western margin of the Caribbean Tethys, to the Eurasian margins of the Mediterranean Tethys and Japan, whereas †*Eodorippe* appears to have been restricted to the Western Pacific realm (Fig. 2.4A, Table 2.1). †*Tepexicarcinus* is only

known from the Gulf of Mexico (Fig. 2.4A). Abundant callianassid chelipedial remains, a mecochirid-like lobster, and a fragmented dorsal carapace of a palaeocorystid crab putatively assigned to †*Joeranina kerri* (Luque *et al.*, 2012) (Fig. 2.3), were found associated with †*Telamonocarcinus antiquus* sp. nov. All three taxa are known to have been infaunal benthos dwellers. Feldmann *et al.* (1998b) and Vega *et al.* (2005) suggested that the morphology of the pereiopods seen in †*Telamonocarcinus gambalatus* and †*Tepexicarcinus tlayuaensis* might indicate that the taxa inhabited shallow marine waters, more likely in coral reefs. †*Telamonocarcinus antiquus* sp. nov. might also have inhabited shallow marine waters, but its occurrence in dark grey, terrigenous, micaceous clay–shales with gypsum indicate that it must have been deposited in low hydrodynamic, poorly oxygenated settings. Although the specimen of †*T. antiquus* sp. nov. might be allochthonous for the faunule, coral reefs from the Paja Formation are unknown, suggesting that the specimen rather inhabited settings proximal to the area of burial.

2.6. Conclusions

Following recent work, and given the nature of the information available, †Telamonocarcinidae is considered to be closer to Dorippidae and Ethusidae than to other brachyuran clades, and reinforces the hypothesis that Dorippoidea is among the most basal groups of eubrachyuran crabs. If this dorippoidean affinity proves to be correct, it would mean that †*Telamonocarcinus antiquus* sp. nov. is together with †*Componocancer roberti* and putatively †*Tepexicarcinus tlayuaensis* the oldest eubrachyuran-like crabs known to date. The broad range of body plans seen among Albian brachyurans indicates that the Early Cretaceous was a time of rapid evolution for crabs, where most of the higher clades (e.g. Raninoida, Cyclodorippoida, †Etyoida, †Torynommoida, Eubrachyura) originated and/or rapidly diversified. Given our current knowledge of the geographic and geological ranges of early eubrachyurans, it can be stated that: a) the oldest eubrachyurans are known from the Americas b) eubrachyurans were already morphologically diverse in Albian times; and c) that their most recent common ancestor most likely is pre–Albian in age, and probably rooted in the earliest Cretaceous or late Jurassic.

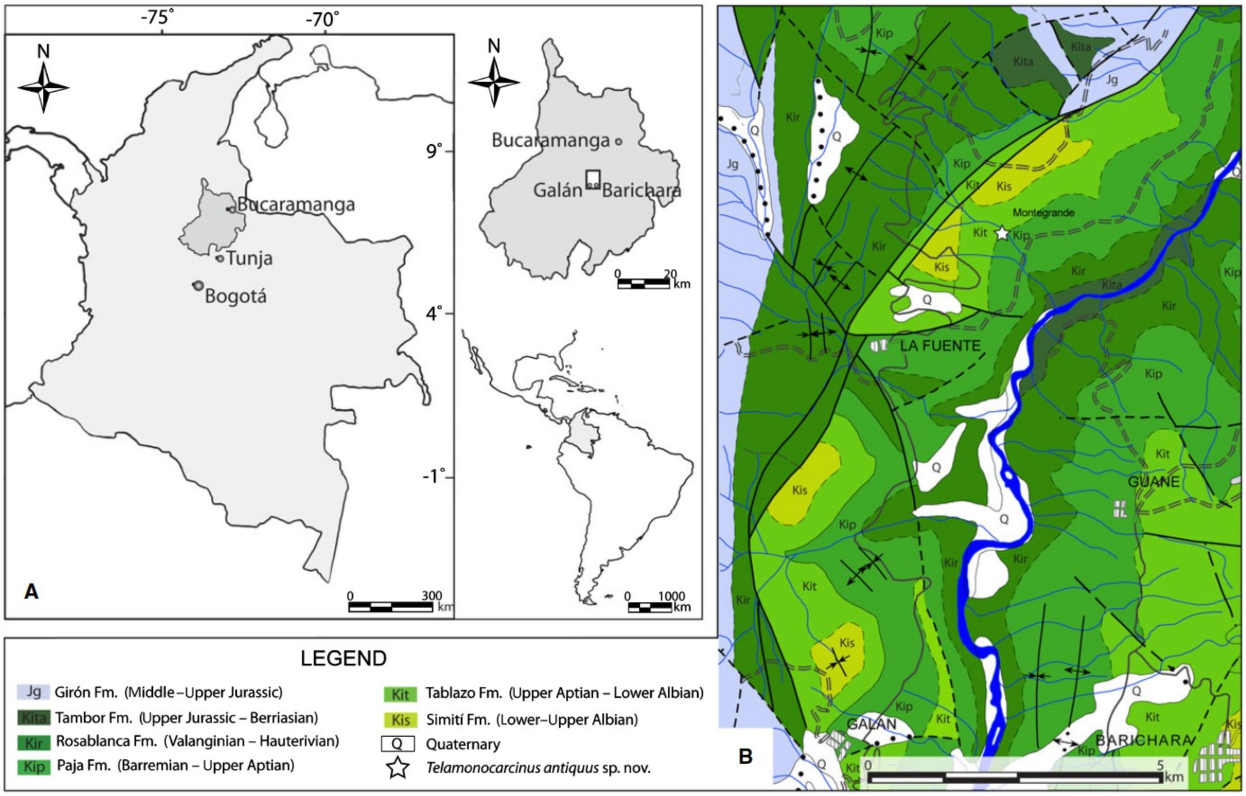


Figure 2.1. A, locality map showing the approximate geographical provenance of †*Telamonocarcinus antiquus* sp. nov., holotype IGM p881012, near the town of La Fuente, Department of Santander, Colombia, South America. B, geological map of the area where the holotype of †*Telamonocarcinus antiquus* sp. nov. was recovered (white star). Abbreviations: J, Jurassic; Ki, Lower Cretaceous; Q, Quaternary. Base map modified from INGEOMINAS Plancha 135 San Gil (after Pulido 1985).

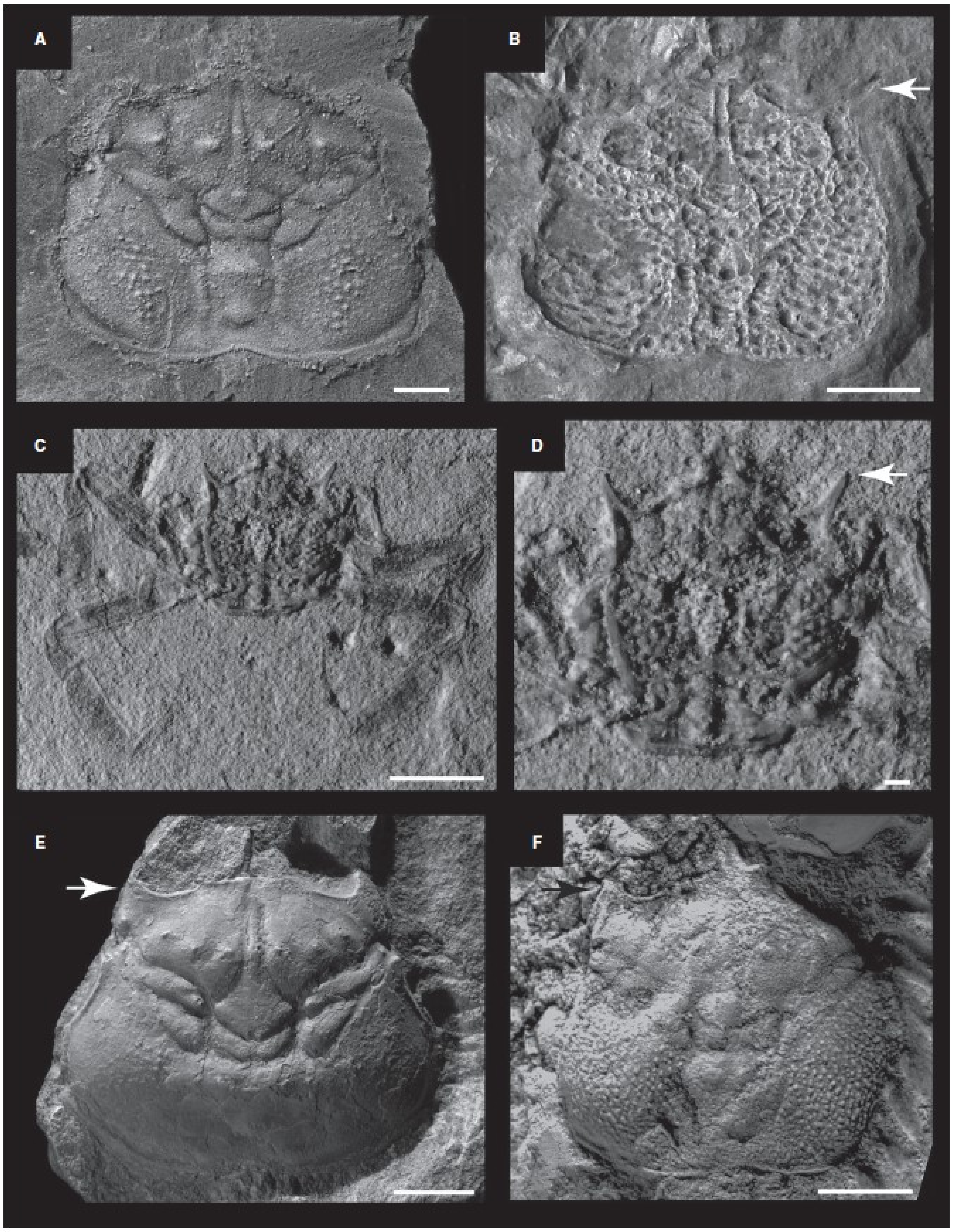


Figure 2.2. Oldest fossil Dorippidea from the Early and Late Cretaceous, family †Telamonocarcinidae. A–D, †*Telamonocarcinus* Larghi, 2004. A, †*Telamonocarcinus antiquus* sp. nov., holotype, IGM p881012, dorsal carapace, Early Albian of Colombia. B, †*T. gambalatus* Larghi, 2004, holotype, MSNMi26033, dorsal carapace, Cenomanian of Lebanon. C–D, †*Telamonocarcinus* sp. specimen MFM247,003, Cenomanian of Japan. E–F, †*Eodorippe* Glaessner, 1980. E, †*E. spedeni* Glaessner, 1980, holotype, N.Z.G.S., AR 675, dorsal carapace, Campanian–Maastrichtian of New Zealand. F: †*E. binodosus* Collins, Kane, and Karasawa, 1993, holotype, MFM247,003, dorsal carapace, Cenomanian of Japan. Arrows indicate the position of large, divergent (†*Telamonocarcinus*) and short, convergent (Eodorippe) outer orbital spines. Scale bars in A, B, and D represent 1 mm, and in C, E, and F represent 5 mm. Images courtesy of Hiroaki Karasawa (C–D, F), Alessandro Garassino (B), and John E. Simes (E).

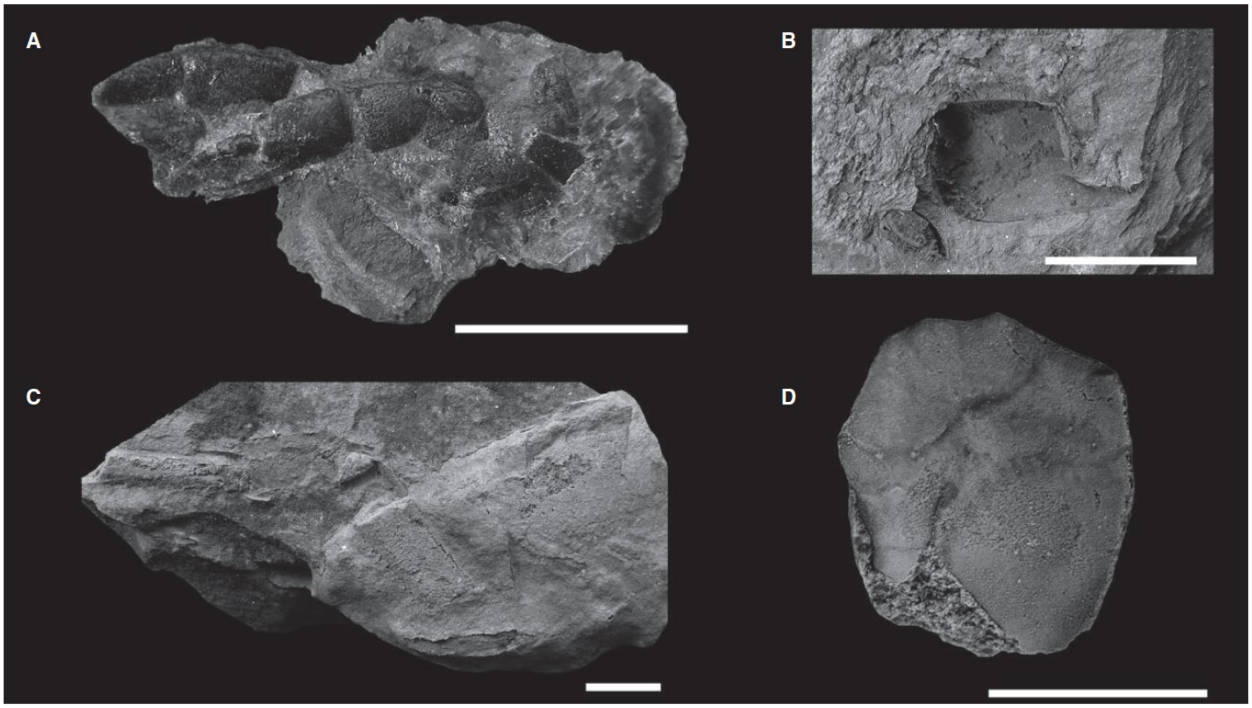


Figure 2.3. Decapod crustaceans from the lowermost Tablazo Formation associated with the holotype of †*Telamonocarcinus antiquus* sp. nov. A–B, callianassid shrimps indet. preserved in gypsum-rich layers; A, specimen IGM p881021, left side of specimen preserving both chelipeds; B, specimen IGM p881018, negative mould of cheliped. C, mecochirid-like lobster, specimen IGM p881014, preserving an elongate and slender first pereiopod. D, †Palaeocorystoidea, †Palaeocorystidae, †*Joeranina* cf. *J. kerri* (Luque et al., 2012), specimen IGM p881013, internal negative mould of anterior right dorsal carapace. All scale bars represent 10 mm.

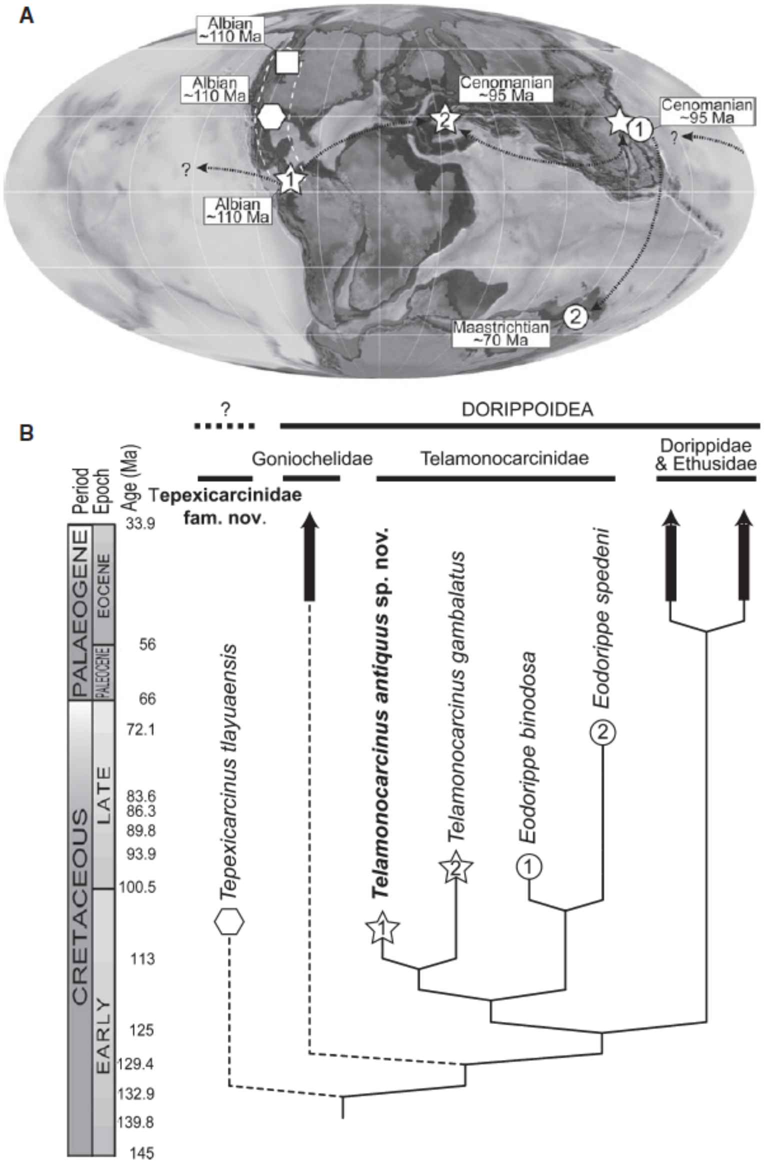


Figure 2.4. Spatial and temporal ranges of the taxa currently included in Telamonocarcinidae and †Tepexicarcinidae fam. nov. A, paleobiogeographic distribution of †*Tepexicarcinus* Feldmann, Vega, Applegate and Bishop, 1998 (hexagon), †*Telamonocarcinus* Larghi, 2004 (stars), and †*Eodorippe* Glaessner, 1980 (circles). Black dotted lines and arrows indicate plausible dispersal routes. White square represents the occurrence of †*Componocancer roberti* Feldmann, Schweitzer, and Green, 2008, which is the oldest confirmed sternitreme eubrachyuran. White dotted line indicates the geographic distribution of the oldest known eubrachyuran and eubrachyuran-like crabs, all from the Early Cretaceous (Albian) of the Americas. Base map for the Early Cretaceous (Aptian. ~120 Ma) modified after Blakey (2006). B, chronostratigraphic distribution of the taxa within †Telamonocarcinidae and †Tepexicarcinidae fam. nov. †Telamonocarcinidae is the only known family of Dorippoidea that lived in the Cretaceous. All other dorippoid families have their oldest representatives in the Eocene, as indicated by †*Ethusa evae* Müller and Collins, 1991 (Ethusidae Guinot, 1977), †*Bartethusa hepatica* Quayle and Collins, 1981 (Dorippidae MacLeay, 1838), †*Goniochele angulata* Bell, 1858, and †*G. madseni* Collins and Jakobsen, 2003 (†Goniochelidae Schweitzer and Feldmann, 2011*b*). Dotted lines indicate the uncertain phylogenetic position of †Goniochelidae among dorippoideans, and the doubtful phylogenetic affinity of †Tepexicarcinidae fam. nov. with Dorippoidea.

Table 2.1. List of known taxa within †Telamonocarcinidae and †Tepexicarcinidae fam. nov.

Taxon	Age (Ma)	Unit	Locality
Telamonocarcinus antiquus sp. nov.	Early Albian (~110)	Lower Tablazo Formation	La Fuente, Santander
Telamonocarcinus gambalatus Larghi, 2004.	Cenomanian to Turonian (~97–90)	'Fish Beds' of western Lebanon	Hgula and Haqil, Lebanon
Telamonocarcinus sp.	Cenomanian (~97)	Mikasa Formation, Middle Yezo Group	Hokkaido, Katsurazawa, Ikushunbetsu, Mikasa City, Japan
Eodorippe binodosus (Collins, Kanie, and Karasawa, 1993).	Cenomanian (~97)	Mikasa Formation, Middle Yezo Group	Hokkaido, Katsurazawa, Ikushunbetsu, Mikasa City, Japan
Eodorippe spedeni Glaessner, 1980.	Campanian–Maastrichtian (~72)	Not specified by author	Stream boulders from bed of Mangahouanga Stream, a tributary of the Te Hoc River, New Zealand
Tepexicarcinus tlayuaensis Feldmann, Vega, Applegate, and Bishop, 1998.	Albian (~110)	Middle Member of the lithographic limestones of the Tlayúa Formation	Tepexi, Mexico
Tepexicarcinidae? genus and species indet. (in Schweitzer *et al.* 2003).	Cenomanian (~96)	Bahariya Formation	Near Gebel el Dist, Egypt

Chapter 3. A puzzling frog crab (Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: Frog first or crab first?

3.1 Introduction

The particular body plan of extant frog crabs has puzzled scientists since Linnaean times, resulting in multiple affiliations with 'higher' and 'podotreme' brachyuran crabs, anomurans, macrurans, and even apterous insects (Linnaeus, 1758; Lamarck, 1801; Latreille, 1802; Milne Edwards, 1837; Dana, 1852; Ortmann, 1892b; Alcock, 1896; Bourne, 1922; Glaessner, 1960, 1969; Števčić, 1973, 1995; Martin and Davis, 2001). They are a group of true crabs, or Brachyura, whose modern representatives are adapted for burrowing in soft to gravelly substrates. Their diagnostic traits, once considered to reflect an ancestral condition (e.g. their elongate carapace, pleon exposed dorsally, narrow sternum and flattened legs), are now thought to be derived adaptations for their burrowing lifestyle, and therefore convergent between several non-related superfamilies of digging anomuran and brachyuran crabs (Borradaile, 1903; Bourne, 1922; Gordon, 1966a; Glaessner, 1969; Števčić, 1973; Williams, 1974; Abele and Felgenhauer, 1982; Dawson and Yaldwing, 2000; Števčić, 2005). The evolutionary origin of raninoidans remains puzzling partly due their astonishing morphological disparity, ranging from broad and heavily ornamented 'crab–looking' families (necrocarcinids and allies), to elongate and smoother 'frog–looking' ones (raninids and allies). Furthermore, an intermediate group, the palaeocorystids, combines plesiomorphic and apomorphic traits seen in both clades, and their phylogenetic affinities are still debated. In addition, the Early Cretaceous has been deemed as the time where the main raninoidan lineages diversified (Karasawa *et al.*, 2011; Luque *et al.*, 2012; van Bakel *et al.*, 2012a), but their scarce fossil record compared to the Late Cretaceous biases our understanding of the polarity of change of certain traits, thus our understanding of their relatedness by common ancestry throughout geological time.

The late Early Cretaceous Santana Group from Brazil, South America is an astonishing fossil-bearing deposit recognized worldwide for extraordinary preservation of marine and terrestrial invertebrates, vertebrates, and plants (Maisey, 1991). Despite the many arthropods found there, only one species of true crab or Brachyura, †*Araripecarcinus ferreirai* Martins–Neto, 1987, has been reported so far. Its holotype and sole specimen was originally described as a dorsal carapace of a portunid crab, a group of higher brachyurans known for their ability to swim with paddle–like posterior legs (Martins Neto, 1987; Maisey, 1991; Maisey and Carvalho, 1995). However, a re-examination of this specimen has revealed that it is neither a portunid crab nor a dorsal carapace with a flattened last pair of legs. This was first noticed by Guinot and Breton (2006) who correctly proposed that †*Araripecarcinus* belonged to Raninoidia, a group of crabs only distantly related to portunids. Karasawa *et al.* (2008) discussed the ventral orientation of the †*Araripecarcinus* type specimen, and based on the shared elongate buccal cavity, the narrow sternum and the posteriorly extended pleon, allied it with Raninidae De Haan, 1839. Since then, †*Araripecarcinus* has been regarded as a raninoidan/raninoidian, although with unclear affinities (Schweitzer *et al.*, 2010; Luque *et al.*, 2012; van Bakel *et al.*, 2012a), which calls for re-examination of the type material, and discussion of the species' systematic relationship with other raninoidans.

This is the first attempt to place †*Araripecarcinus* in synthetic and cladistic contexts, and discuss its implications for frog crab phylogenetic relationships.

3.2. Results

3.2.1. Systematic palaeontology

Decapoda Latreille, 1802

Brachyura Linnaeus, 1758

Family uncertain

†***Araripecarcinus*** Martins–Neto, 1987

Type species. †*Araripecarcinus ferreirai* Martins–Neto, 1987, by monotypy.

Emended Diagnosis. Carapace subcircular in outline, nearly as wide as long, as seen in †Necrocarcinidae Förster, 1968, †Cenomanocarcinidae Guinot, Vega and Van Bakel, 2008; †Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg and Ross, 2003, and †Camarocarcinidae Feldmann, Li and Schweitzer, 2007; maximum width near to midlength; pterygostome broad, vaulted, crest inconspicuous, surface granulated; anterolateral and posterolateral margins convex, both apparently lacking spines; cervical groove reaching ventral carapace; buccal cavity elongated, about half the carapace length. Thoracic sternum narrow; S3 distinct ventrally, wider than long; S4 flattened mesially, lateral margins sub–parallel and slightly convex; E4 longer than wide, slightly ovate distally, forming with lateral margins of S4 an angle of ~120 degrees; suture 4/5 incomplete; S5 similar in shape to S4; suture 5/6 incomplete; S6 separated in anterior and posterior plates by a weak, transverse fracture point; sterno–coxal depression absent; thoracic sexual openings absent; sternal pleon locking mechanisms on E5 absent in holotype. Chelipeds (Ch) isochelous; P2 and P3 the longest of all pereiopods, similar in size; P4 nearly half P2–P3; P5 the smallest, very reduced, apparently sub–dorsal.

Geologic range. Late Early Cretaceous (Albian) of Araripe Basin, Brazil.

Remarks. The original assignment of †*Araripecarcinus* within Portunoidea Rafinesque, 1815, was founded on the presumed possession of a P5 adapted for swimming as seen in most portunoids, and different enough from the ‘flattened and foliaceous’ pereiopods seen in extant members of Raninoidea (Martins-Neto, 1987, p. 408). However, what he considered to be flattened sclerites of P5, actually correspond to the carpus and the apparently flat propodus of P4, whereas P5 is very reduced and apparently carried subdorsally (Figs 3.1B, 3.2A). In addition, the ‘portunid branchial lobes’ depicted by Martins–Neto (1987, fig. 2), are the arthrodial cavities of the chelipeds; the ‘epibranchial’ and ‘mesogastric’ regions are the pterygostome and the buccal cavity respectively; and the ‘urogastric’, ‘cardiac’ and ‘intestinal regions’ are part of the thoracic sternum (Figs 3.1A–B, 3.2A–B). Furthermore, Martins–Neto stated that †*Araripecarcinus* “is clearly related to the torynommid genus †*Mithracites* from the Aptian of England” (Martins–Neto, in Maisey, 1991, p. 411). Currently, †*Mithracites* Gould, 1859, is regarded as closer to homoloidans than to torynommoidans (Guinot and Tavares, 2001; Števčić, 2005; Karasawa *et al.*, 2011; Schweitzer and Feldmann, 2011b; van Bakel *et al.*, 2012b), and based on the diagnostic traits seen in the type material of †*Araripecarcinus*, affiliation with portunoids, homoloids or torynommoids is untenable.

Among podotreme crabs, †*Araripecarcinus* traits are reminiscent of those present in the raninoidan families †Camarocarcinidae and †Necrocarcinidae, especially the roundish carapace outline, the morphology of the thoracic sternum, and the cervical groove reaching ventrally (Fig. 3.1A–B). †*Araripecarcinus*, however, lacks the grooved pterygostome seen in camarocarcinids, with a long blunt crest, the strongly concave thoracic sternum and the sterno–pleonal depression (van Bakel *et al.*, 2012a). Its episternites are more broadly spaced from each other than other palaeocorystoids, the S4 has sub–parallel and slightly convex lateral margins, and forms with the anterior margin of E4 an angle of nearly 120 degrees (Fig. 3.2B). Moreover, its paleogeographic and stratigraphic range contrast with those of typical camarocarcinids, exclusively known from Paleocene rocks of North Dakota, Greenland, and Denmark (Holland and Cvancara, 1958; Feldmann *et al.*, 2007; Guinot *et al.*, 2008; van Bakel *et al.*, 2012a), further casting doubts of any camarocarcinid relationship. This does not rule out that camarocarcinids might have Cretaceous representatives from low latitudes, but no such fossil has been found to date.

Following the works of Karasawa *et al.* (2011) and van Bakel *et al.* (2012a), the presence of a double protrusion mechanism on E5 for pleon holding seen in †Orithopsidae and †Cenomanocarcinidae, their broad S4 with large and wide E4 (Fig. 3.3), their generally sub–hexagonal carapaces, and the cervical groove ending anterior to the spinose anterolateral margins, rule out affiliation with †*Araripecarcinus*. Its ventral architecture is more reminiscent of some necrocarcinids, especially that of †*Planocarcinus* Luque, Feldmann, Schweitzer, Jaramillo and Cameron, 2012, as seen in †*P. johnjaghti* Bermudez, Gómez–Cruz and Vega, 2013 (Bermúdez *et al.*, 2013). The authors commented on the post–rostral slits present on *P. olssoni* (Rathbun, 1937), which are distinctive, although not exclusive, of the paranecrocarcinid–like taxa, since some palaeocorystids also bear them (van Bakel *et al.*, 2012a).

†*Araripecarcinus* might well belong to the same stock as planocarcinids or paranecrocarcinids, but its unknown dorsal carapace, together with the poorly known sternal

architecture of necrocarcinids and paranecrocarcinids (Feldmann *et al.*, 2007; Jagt *et al.*, 2010; van Bakel *et al.*, 2012a), obscures its familiar placement.

3.2.2. Phylogenetic analysis

The analyses were performed using a modified dataset after Karasawa *et al.* (2011), containing 16 taxa and 44 adult morphological characters. Additional raninoidan taxa included are Lyreididae Guinot, 1993, and †Orithopsidae, scored after van Bakel *et al.* (2012a), plus the genus †*Araripecarcinus*, and the eubrachyuran family Portunidae, to which †*Araripecarcinus* was originally affiliated (Martins Neto, 1987). The dataset was produced in Mesquite (Maddison and Maddison, 2011), and the phylogenetic analysis was conducted in TNT 1.1 (Goloboff *et al.*, 2008b). All characters were unordered and equally weighted. Branch supports were obtained in Mesquite. Traditional search for sub–optimal trees included 1000 replicates, and Implicit enumeration search was performed without collapsing trees after the search. Both searches lead to the same tree topologies. Bootstrap and Jackknife values were obtained after 1000 replicates each. Bremer support values for the Traditional search were calculated under tree bisection reconnection (TBR), and retained trees suboptimal by 30 steps. Since †*Araripecarcinus* dorsal traits are unknown, and its familiar placement uncertain, two analyses were performed excluding and including †*Araripecarcinus*, respectively, to evaluate the internal relationships of raninomorph families (Fig. 3.4).

The first phylogenetic analysis, excluding †*Araripecarcinus*, yielded three equally most parsimonious trees, with T.L. = 81 steps; C.I. = 0.85; and R.I. = 0.87 (Fig. 3.4A). In the strict consensus, the clade Raninomorpha is constituted by the branches derived from the most recent common ancestor for all fossil and extant frog crabs and allies (raninoidans/raninoidians) (Figs 4A, 5). They are united by the possession of an elongate buccal cavern, an mp3 lying in two planes, and a P5 is reduced and carried in a more dorsal position than P4 (Karasawa *et al.*, 2011; van Bakel *et al.*, 2012a). Within Raninomorpha, two main clades are clearly distinguishable; one containing the raninid–like taxa, or Raninoidea, and the other containing the necrocarcinid–like taxa, or Necrocarciniformes (Fig. 3.5). Raninoidea is the clade stemming from the most recent common ancestor for lyreidids, raninids, symethids, all of them known from fossil and extant taxa. They seem to share a long carapace, with straight to convex posterior margins, bearing narrow to reduce posterior sternites, and a presumed united spermatheca (Karasawa et al. 2011). The palp of their mxp3 is carried in an inner mesial position, and they have partially exposed pleurites associated to sterno–pleural extensions (van Bakel *et al.*, 2012a. Necrocarciniformes is the clade stemming from the most recent common ancestor for necrocarcinids, cenomanocarcinids, and orithopsids (Figs 3.4A, 5). Necrocarciniforms are confined to the fossil record, ranging from the Early Cretaceous to the Paleogene, and they differ from Raninoidea mainly, but not exclusively, in their broader carapaces, and the presence of branchial longitudinal ridges or rows of tubercles Karasawa *et al.*, 2011; van Bakel *et al.*, 2012a. In this analysis, the necrocarciniform terminals were recovered in a soft polytomy. Necrocarciniformes also lies in a soft trichotomy with †Camarocarcinidae and the clade uniting Palaeocorystidae and Raninoidea (Fig. 3.4A). Under this scenario, the superfamily Palaeocorystoidea would represent a paraphyletic assemblage.

The second phylogenetic analysis, including †*Araripecarcinus*, produced one most-parsimonious tree, with T.L. = 81 steps; C.I. = 0.85; and R.I. = 0.87 (Fig. 3.4B). Despite the large number of unknown character states in †*Araripecarcinus*, the tree topology is better resolved with all polytomies dissolved. In this analysis, the clade (†*Araripecarcinus* (†Camarocarcinus (†Palaeocorystidae (Raninoidea)))) is united by the wide or flattened P2 to P4, and is recovered as sister to Necrocarciniformes. However, this trait is homoplasious since †Cenomanocarcinidae also have wide or flattened P2 to P4. †*Araripecarcinus* is recovered as sister taxon to the clade (†Camarocarcinidae (†Palaeocorystidae (Raninoidea))), which is united by the presence of an indistinct or faint cervical groove. This character is polymorphic on †Cenomanocarcinidae and †Palaeocorystidae, as it is in the sister group to Raninomorpha. The clade (Palaeocorystidae (Raninoidea)) is united by the shared elongate carapace, which is an apomorphic condition among raninomorphs. It is possible that Symethidae Goeke 1981 constitutes a subfamily within Raninidae, rather than its sister taxon, as initially envisioned by Goeke (1981) (see Guinot, 1993; Ahyong *et al.*, 2007; van Bakel *et al.*, 2012a).

3.3. Discussion

Extant frog crabs are exclusively marine, ranging from very shallow subtidal bottoms to nearly 1,400 m depth (Tucker, 1995). Similarly, their fossils are known from marine rocks worldwide, and no taxon has been reported from freshwater settings. This suggests that †*Araripecarcinus* was a marine dweller, as hypothesized by Martins–Neto (1987, p. 409). It was found in the same concretion with the aspidorhynchid fish †*Vinctifer comptoni* (Agassiz, 1841), one of the most abundant fishes in the Romualdo Member, and considered to be a brackish to marine form (Martins-Neto, 1987; Maisey, 1991; Maisey and Carvalho, 1995). Based on palynomorphs, a mid–late Albian age has been assigned to the *Vinctifer*–bearing horizons, and hence to the †*Araripecarcinus* specimen (Pons *et al.*, 1990; Moody and Maisey, 1994). Although †*Araripecarcinus* is the only adult brachyuran known from the Santana Group, and therefore the Romualdo Formation, a few brachyuran zoea larvae are known from stomach contents of the fish *Tharrhias araripis* Jordan and Branner, 1908; a presumed plankton feeder (Maisey, 1994; Maisey and Carvalho, 1995). One larva (Fig. 3.6) seemingly lacks lateral spines, and bears short rostral and dorsal spines –the latter apparently broken, that are shorter than the carapace length. This is the only fossil record of brachyuran protozoeal larva known to date (Maisey and Carvalho, 1995). In the extant frog crab *Ranina ranina* (Linnaeus, 1758), instars I to VIII retain large rostral and dorsal spines, but lateral spines become faint to inconspicuous in late stages (Rice and Ingle, 1977; Minagawa, 1990). Whether the fossil larva belong to a raninomorph, and particularly to †*Araripecarcinus*, remains uncertain, but it clearly indicates that brachyurans were present in the shallow marine to brackish waters of the Araripe Basin during the Albian, and that they might have played an important role as food items at different ontogenetic stages (Maisey and Carvalho, 1995).

As in extant raninomorphs, the flattened articles of P2 to P4 of †*Araripecarcinus* might have assisted in burrowing, and even occasionally swimming (Guinot *et al.*, 2008, p. 688). The shape and proportions of P4 in raninomorphs can vary from a P4 slightly shorter than P2–P3 to nearly as reduced as P5, and scoring these characters in further phylogenetic analyses should reflect such variation in sizes. The clades including †*Araripecarcinus* and †Camarocarcinidae are poorly supported, and although both terminals were recovered as closer to Palaeocorystidae + Raninoidea, it is likely that it is an artefact of their number of unknown character states, being actually more related to Necrocarciniformes. Under either phylogenetic scenarios, the superfamily †Palaeocorystoidea is paraphyletic, and suggest that the plesiomorphic condition for raninomorphs is to have broader carapaces, indicating that the innovation of an elongated carapace might have occurred only once in the evolutionary history of Raninomorpha, and likely to have been present in the last common ancestor for †Palaeocorystidae, Lyreididae, Raninidae and Symethidae. Due to the incompleteness of †*Araripecarcinus*, it is impossible for me to warrant its familial or superfamilial placement, although the general sternal configuration and carapace proportions are reminiscent of some necrocarcinids. †Camarocarcinidae was recovered as the sister taxon to the clade (†Palaeocorystidae (Raninoidea)) principally due its lack of branchial ridges or rows of tubercles, as seen among necrocarciniforms. This might imply that a) the lack of branchial ornamentation is the plesiomorphic condition for Raninomorpha, and such innovation only evolved once in the most recent common ancestor for Necrocarciniformes, or b) that Camarocarcinidae, if assuming it is closer to Necrocarciniformes than to Palaeocorystidae + Raninoidea, might have secondarily lost them (reversal).

Despite frog crabs *sensu lato* being considered as a monophyletic group, there is no agreement on whether they constitute a section (Raninoida) or a subsection (Raninoidia) within the Infraorder Brachyura (Ahyong *et al.*, 2007; Guinot *et al.*, 2008; De Grave *et al.*, 2009; Schweitzer *et al.*, 2010; Karasawa *et al.*, 2011; Ahyong *et al.*, 2012; van Bakel *et al.*, 2012a). This is a non–trivial issue, since each rank underlies alternative hypotheses regarding the monophyly or paraphyly of Podotremata Guinot (1977), and therefore the evolutionary relationships among the main brachyuran lineages (Tavares, 2003; Ahyong *et al.*, 2007; De Grave *et al.*, 2009; Karasawa *et al.*, 2011). For this reason, I refer to raninoidans/raninoidians as Raninomorpha, an unranked monophyletic clade that contains all the descendants from the most recent common ancestor for all frog crabs and allies, independent of taxonomic rank. Also, the families †Necrocarcinidae, †Cenomanocarcinidae and †Orithopsidae are distinctive enough to be grouped together, but since no taxonomic rank lies between family and superfamily to accommodate the necrocarcinid–like families, I refer to them as Necrocarciniformes, an unranked monophyletic clade that contains all the descendants from the most recent common ancestor for †Necrocarcinidae, †Cenomanocarcinidae and †Orithopsidae.

Although raninomorph families tend to be distinctive from each other, their phylogenetic relationships at the generic level remain unexplored.

3.4. Conclusions

Based on comparative anatomy and phylogenetic analyses, †*Araripecarcinus* is included within the unranked clade Raninomorpha, a higher clade of brachyuran crabs that embraces the same terminals included under the taxonomic ranks Raninoida and/or Raninoidia. †*Araripecarcinus*, recovered as sister taxon to the clade uniting Camarocarcinidae, Palaeocorystidae and Raninoidea, supports the hypothesis that the plesiomorphic condition for raninomorphs is to have broad carapaces rather than elongate ones. However, due its large number of unknown character states, its superfamilial and familial placement is still uncertain, and based solely on the observed ventral traits, †*Araripecarcinus* was likely closer to Necrocarciniformes than to Palaeocorystidae.

Necrocarciniformes include some of the oldest raninomorphs known to date (Hauterivian to late Aptian, ~132 to ~115 Ma.), providing further evidence that a more 'crab–like' body plan was the ancestral condition for Raninomorpha. The key innovation of elongated carapaces, as seen in Palaeocorystidae, appears in the fossil record not long after some ancient necrocarciniforms (late Aptian, ~115 Ma.), followed by the oldest raninoids (mid Albian, ~108 Ma.), and should have been present in the most recent common ancestor for Palaeocorystidae and Raninoidea. Under this scenario, the earliest palaeocorystids must have derived from a necrocarciniform–like ancestor, but once they occupied a new morphospace, they marked the evolutionary beginning of Raninoidea. Such transition from 'crab–like' to 'frog–like' carapaces could be related to their burrowing lifestyle, raising the question if all raninomorphs were burrowers, or if some ancient necrocarciniform lineages were mostly epibenthic. Phylogenetic analyses at the generic level are needed in order to evaluate the position of Palaeocorystidae with respect to Necrocarciniformes and Raninoidea, helping to better resolve the raninomorph evolutionary tree of life, and to gain a broader understanding on their relatedness by common ancestry throughout geological time.

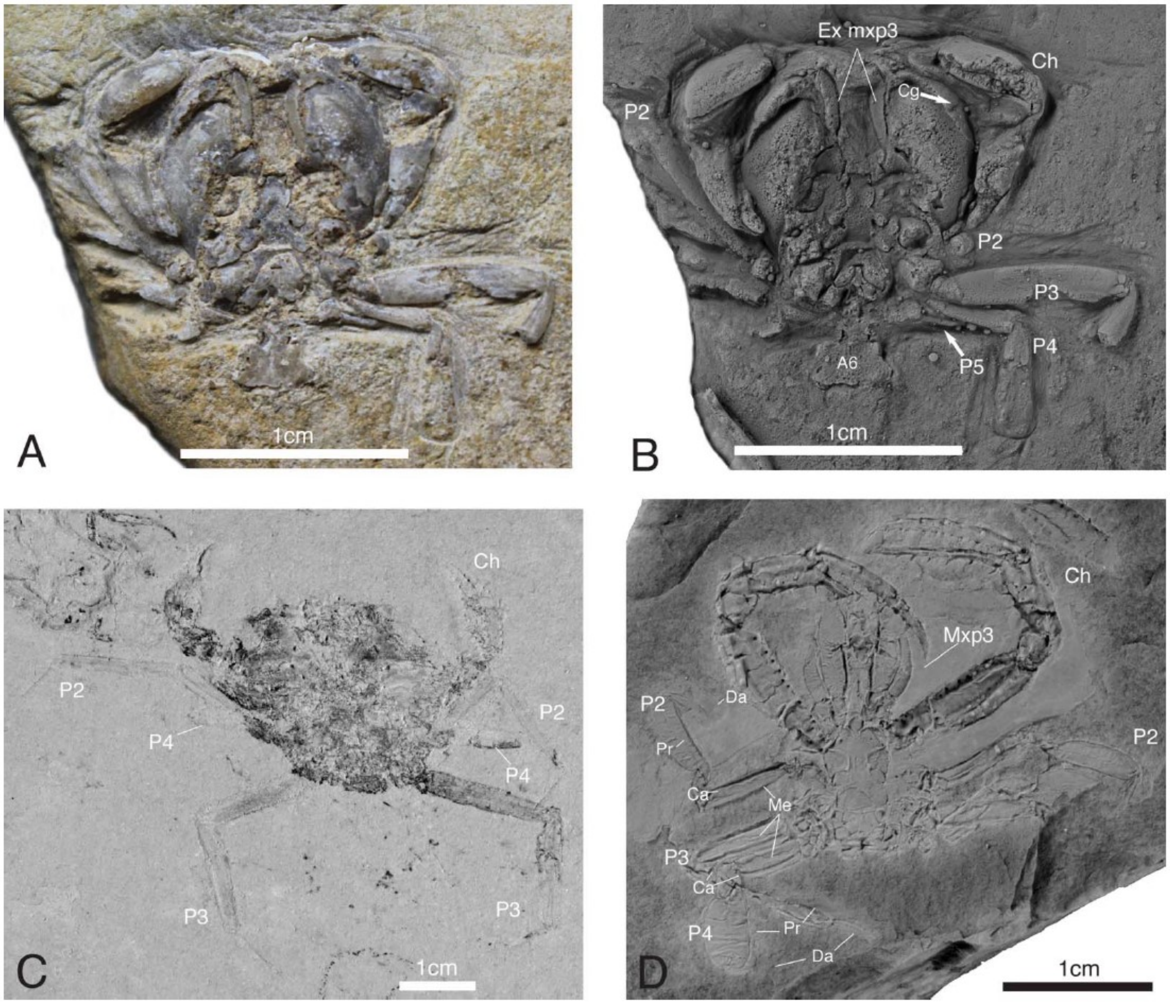


Figure 3.1. Fossil Necrocarcinoidea preserving sternal features. A–B, †Necrocarcinoidea incertae sedis: †*Araripecarcinus ferreirai* Martins–Neto, 1987, Albian of Brazil. A, ventral view of holotype USP (GP/1T 1477); B, cast of holotype coated with ammonium chloride. C, †Necrocarcinidae: †*Corazzatocarcinus* sp., ventral view of specimen UF110982, Cenomanian of Lebanon. D, †Cenomanocarcinidae: †*Cenomanocarcinus* sp., ventral view of specimen IGM p880291, Turonian of Colombia (Luque et al, in progress). Abbreviations: A6, sixth pleonite; Ca, carpus; Cg, cervical groove reaching ventral carapace; Ch, cheliped; Da, dactylus; Ex mxp3, exopods of third maxilliped; Me, merus; Mxp3, third maxillipeds; P2–P5, pereiopods two to five; Pr, propodus.

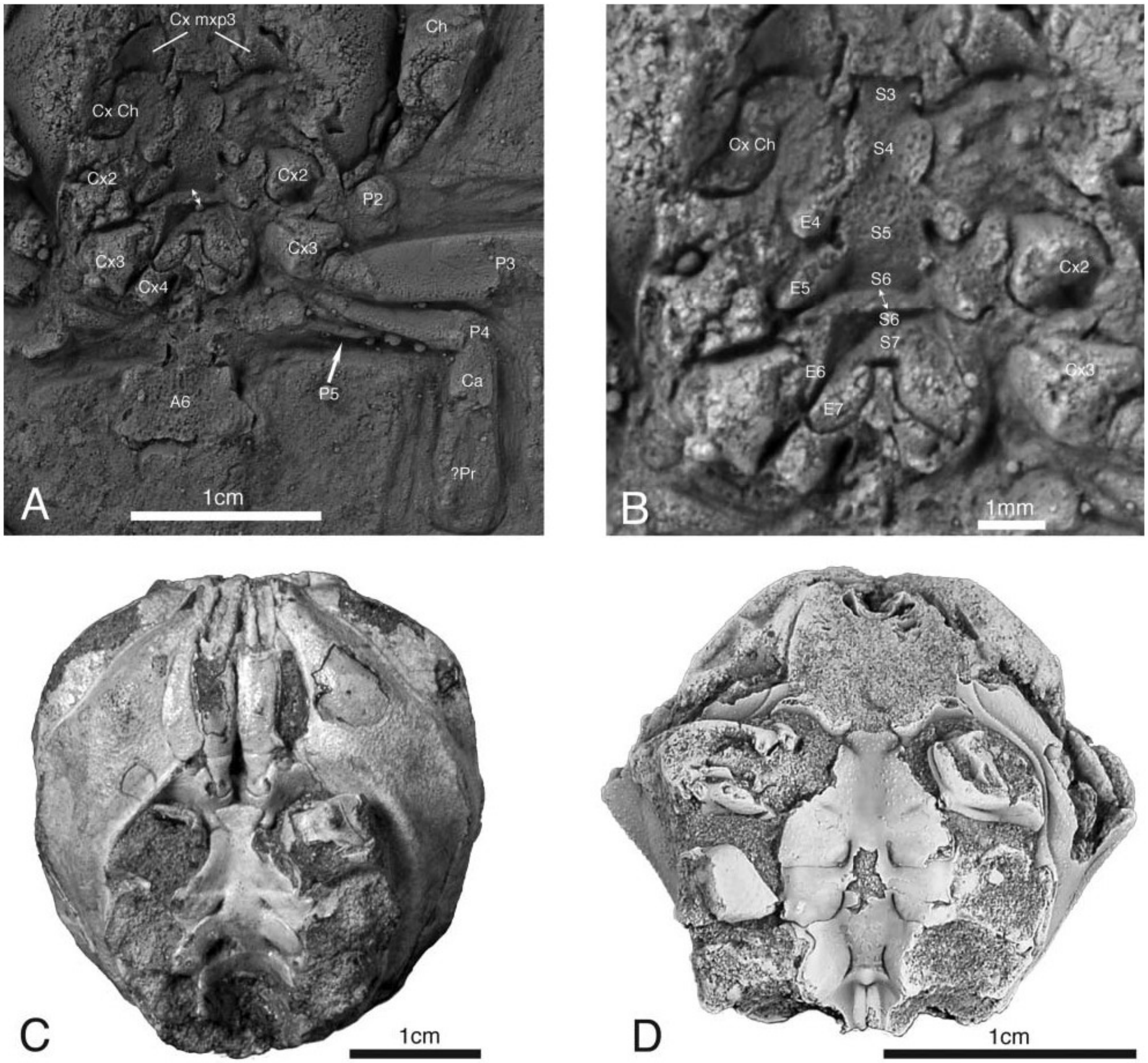


Figure 3.2. Fossil Necrocarcinoidea preserving sternal features (cont.). A–B, †Necrocarcinoidea incertae sedis: †*Araripecarcinus ferreirai* Martins–Neto ,1987, cast of holotype USP (GP/1T 1477), Albian of Brazil. A, ventral view showing the position of chelipeds, pereiopods, and pleonite 6; B, close up of fig. 2A, showing details of the thoracic sternum; C, †Camarocarcinidae: †*Camarocarcinus arnesoni* Holland and Cvancara, 1958, hypotype USNM 103624, ventral view, Upper Cretaceous of North Dakota, USA; D, †Orithopsidae: †*Silvacarcinus laurae* Collins and Smith, 1993, ventral view of holotype IRScNB TCCI 6115, Lower Eocene (Ypresian) of Belgium (reproduced from Van Bakel *et al*. 2012, fig. 21a, Zootaxa 3215 with permission from Magnolia Press). Abbreviations: A6, sixth pleonite; ?Pr, ?propodus of P4; Ca, carpus; Ch, cheliped; Cx mxp3, coxa of third maxilliped; Cx2–Cx4, coxae of P2 to coxa of P4; Da, dactylus; E4–E7, episternites four to seven; Me, merus; P2–P5, pereiopods two to five; Pr, propodus; S3–S7, sternites three to seven.

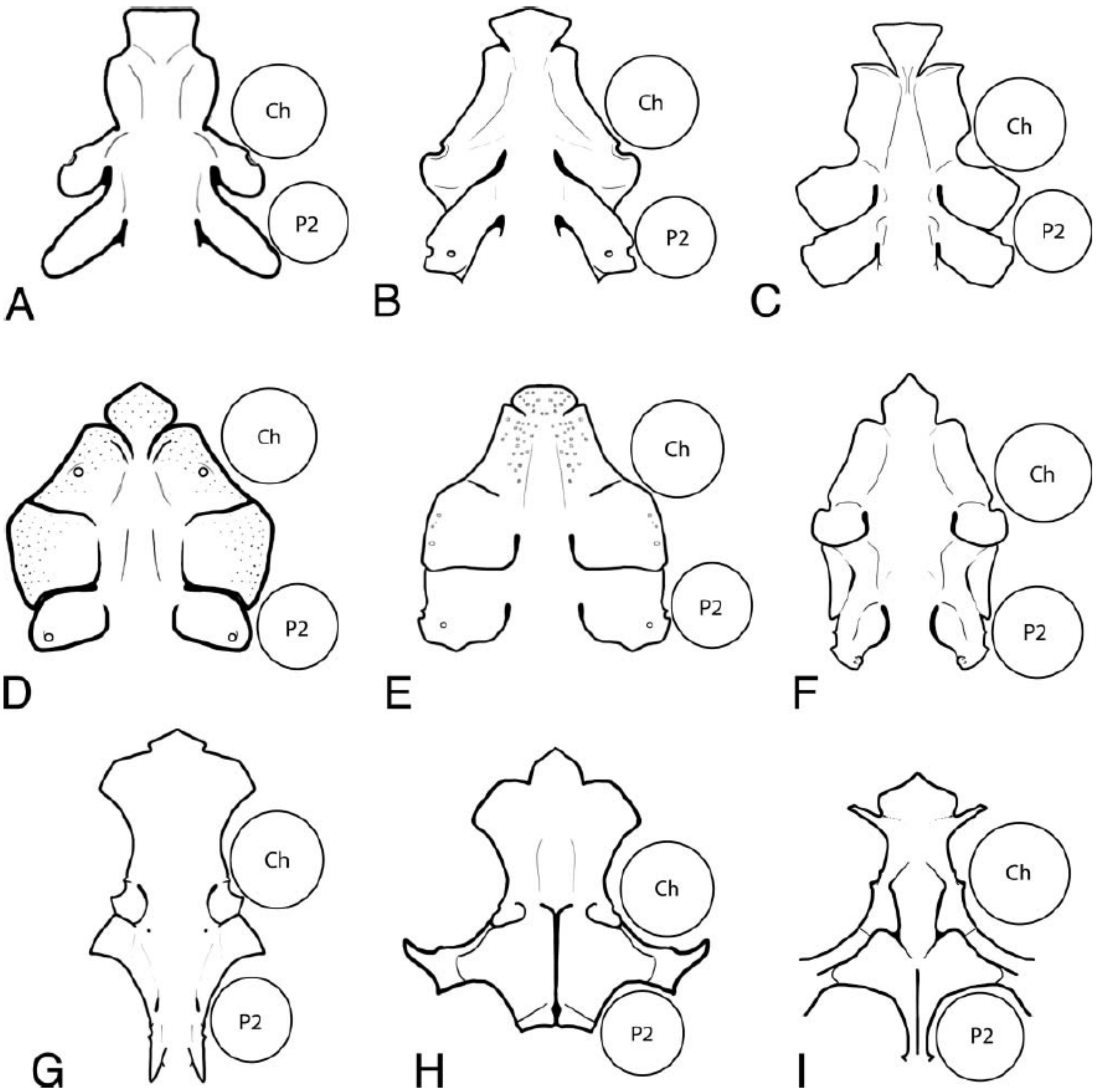


Figure 3.3. General sternal configuration in †*Araripecarcinus* Martins–Neto, 1987, and representatives of the eight fossil and extant terminals of Raninomorpha. A–E, †Necrocarcinoidea. A, †Necrocarcinoidea incertae sedis: †*Araripecarcinus ferreirai* Martins–Neto, 1987 (Figs 1A–B, 2A–B); B, †Camarocarcinidae: †*Camarocarcinus arnesoni* Holland and Cvancara, 1958 (Fig. 2C); C, †Necrocarcinidae: †*Necrocarcinus labeschei* (Eudes–Deslongchamps, 1835) (after Karasawa *et al*. 2011, fig. 10B); D, †Cenomanocarcinidae: †*Cenomanocarcinus* sp. (Fig. 1D); E, †Orithopsidae: †*Silvacarcinus laurae* Collins and Smith, 1993 (Fig. 2D); F, †Palaeocorystoidea, †Palaeocorystidae Lőrenthey, in Lőrenthey and Beurlen, 1929, †*Notopocorystes stokesii* (Mantell, 1844) (after Van Bakel *et al*. 2012, fig. 37A). G–I, Raninoidea. G, Lyreididae: *Lyreidus tridentatus* de Haan, 1841 (after Feldmann and Schweitzer 2007, fig. 4B); H, Raninidae: *Raninoides* sp.; I, Symethidae, *Symethis* sp. Abbreviations: Ch, cheliped; P2, second pereiopod. The circles indicate the approximate location of coxae of Ch and P2.

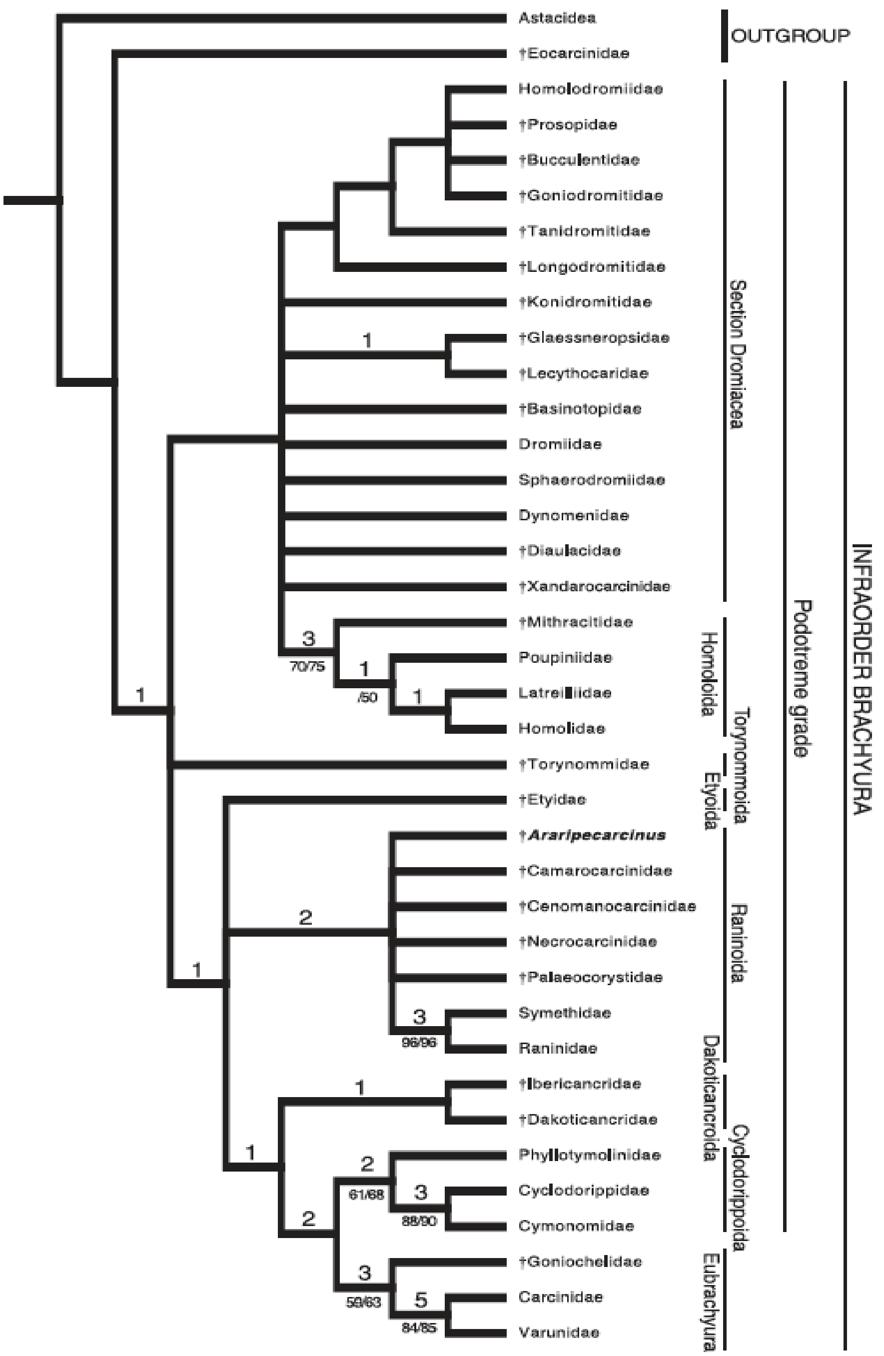


Figure 3.4. Phylogenetic analyses excluding (I) and including (II) †*Araripecarcinus* Martins–Neto, 1987, respectively. A, analysis I, strict consensus of the single most parsimonious tree, with treelength (T.L.) = 81 steps; consistency index (C.I.) = 0.85; retention index (R.I.) = 0.87. B, analysis II, strict consensus trees of seven equally most parsimonious trees, with treelength (T.L.) = 81 steps; consistency index (C.I.) = 0.85; retention index (R.I.) = 0.87. Bremer support indicated above the branches, and Bootstrap/Jackknife values indicated below the branches, respectively. Terminal taxa indicated by † known only from fossil representatives.

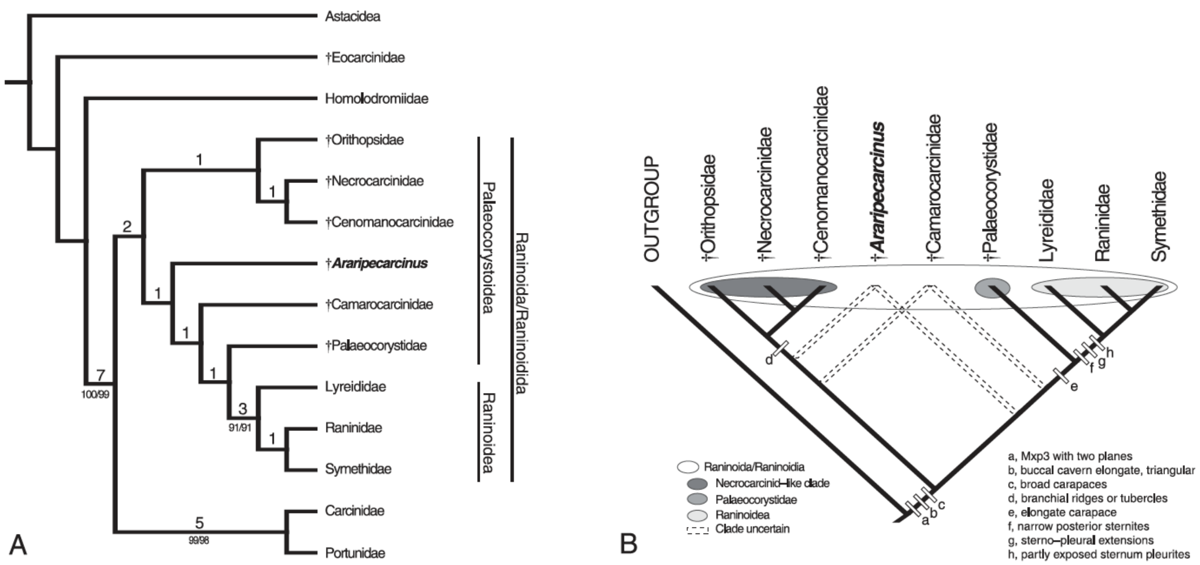


Figure 3.5. Phylogenetic tree (A) and cladogram (B) showing the three main clades constituting the monophyletic Raninomorpha clade (white oval). Necrocarciniformes new clade (dark grey oval), embracing those raninomorph terminals with usually broad, highly ornamented carapaces with defined cervical and branchiocardiac grooves, and bearing branchial ridges or tubercles; i.e. †Necrocarcinidae Förster, 1968, †Cenomanocarcinidae Guinot, Vega and Van Bakel, 2008; and †Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg and Ross, 2003. †Palaeocorystidae Lőrenthey, in Lőrenthey and Beurlen, 1929 (grey oval), includes taxa with a somewhat 'frog–like' appearance, typically longer than wide, with carapaces varying from highly to poorly ornamented, and having well defined to faint cervical and branchiocardiac grooves. Raninoidea De Haan, 1839 (light grey oval) embraces those raninomorphs with typical 'frog–like' longer carapaces, usually poorly ornamented to smooth, and with overall faint to incipient dorsal grooves. Camarocarcinidae Feldmann, Li and Schweitzer, 2007, and †*Araripecarcinus* Martins–Neto, 1987 (dotted line) have dubious phylogenetic placement due their number of unknown character states, particularly †*Araripecarcinus*. Main raninomorph apomorphies indicated by white bars and letter a to h. Terminal taxa indicated by a dagger (†) only known from fossil representatives. Base tree after fig. 4B.

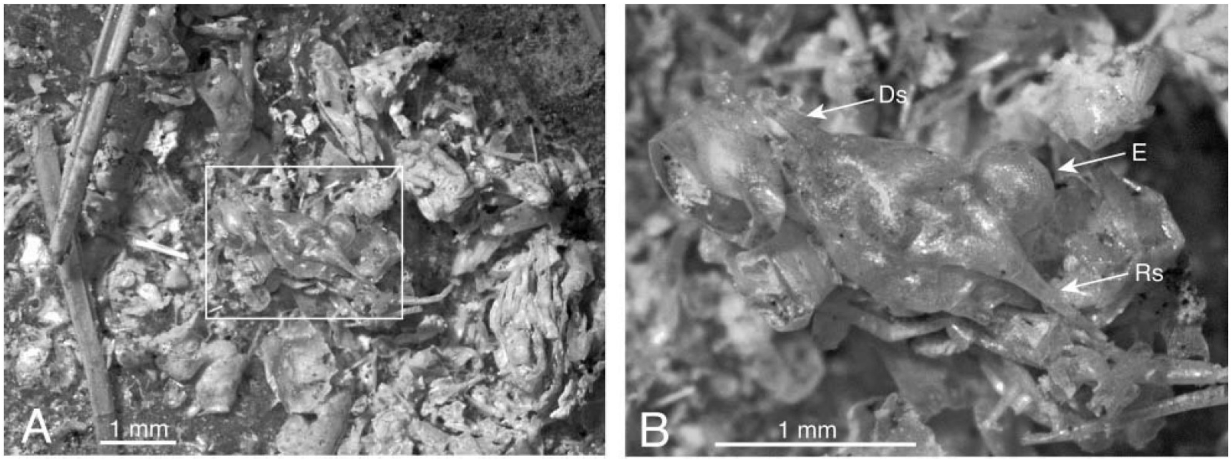


Figure 3.6. Fossil brachyuran crab zoea, AMNH 80038, from the upper Aptian-lower Albian Romualdo Formation, Araripe Basin, Brazil, recovered as stomach contents from the fish †*Tharrhias araripis* Jordan and Branner, 1908, AMNH FF 13680 (see Maisey 1994, fig. 10; Maisey and Carvalho 1995, fig. 4), Abbreviations: Ds, dorsal spine; E, left compound eye bearing facets; Rs, rostral spine.

Chapter 4. Exceptional preservation of a chimaera crab from the Cretaceous reveals a novel body form and mode of life in early crabs

4.1 Introduction

Crabs are a speciose and economically important group of crustaceans that, due to physiological flexibility and the highly diverse morphology of their modular exoskeletons, have colonized marine, fresh-water, and terrestrial habitats worldwide. Although the oldest decapod crustaceans, are first known from the Late Devonian (~360 Ma) (Schram *et al.*, 1978; Feldmann and Schweitzer, 2010a; Gueriau *et al.*, 2014; Jones *et al.*, 2014), the more derived groups of decapods did not evolve and radiate until the Mesozoic: false crabs and squat lobsters, collectively called Anomura (Late Triassic, ~210 Ma) (Chablais *et al.*, 2011) and true crabs, or Brachyura (Early Jurassic, ~170 Ma) (Schweitzer *et al.*, 2010; Karasawa *et al.*, 2011; Tsang *et al.*, 2014). In fact, the extensive radiation of crabs and the beginning of their considerable ecological impact, either as prey or predators, occurred during the 'Mesozoic Marine Revolution' of the Late Jurassic–Early Cretaceous (160–100 Ma) (Vermeij, 1977; Schweitzer and Feldmann, 2010b; Klompmaker *et al.*, 2015b; Schweitzer and Feldmann, 2015). During this time several groups diversified into distinctive adaptive zones, including inhabiting empty gastropod shells, carrying other organisms for camouflage, cryptic fossorial lifestyles, and even facultative and active swimming.

Today, more than 10,000 species of fossil and extant Brachyura (Ng *et al.*, 2008; Schweitzer *et al.*, 2010; Tsang *et al.*, 2014), are grouped into eight major groups defined mainly by the shape of their carapace, claws, mouthparts, locomotory appendages, pleon, and position of sexual openings (Guinot, 1977; De Grave *et al.*, 2009; Karasawa *et al.*, 2011; Guinot *et al.*, 2013). The two earliest branching lineages of living Brachyura, sponge crabs (Dromiacea) and carrier crabs (Homoloida), are first known from the Middle-Upper Jurassic of Europe and Tanzania (~170–150 Ma) (Krobicki and Zatoń, 2008; Schweitzer and Feldmann, 2010c; Schweigert and Koppka, 2011). But brachyuran anatomical and ecological diversity exploded during the Cretaceous, as indicated by the oldest records of the remaining crab clades: extant crown-group frog crabs (Raninoida), cyclodorippoids (Cyclodorippoida), and 'higher' true crabs (Eubrachyura), plus at least three extinct lineages (e.g., Etyoida, Torynommoida, and Dakoticancroida); all first known from Europe, Australia, North America, and more recently from South America (~130–75 Ma) (Karasawa *et al.*, 2011; Luque, 2015b; Luque *et al.*, 2017b). Both molecular and morphological phylogenies indicate that Brachyura is monophyletic, and sister to Anomura (Ahyong *et al.*, 2007; Karasawa *et al.*, 2011; Tsang *et al.*, 2014), but phylogenetic relationships among the main brachyuran taxa remain unsettled largely due the lack of early, intermediate body forms. Further complicating matters, although the tropics today hold a large part of the world's biodiversity (Jablonski, 1993; Jablonski *et al.*, 2006; Martin *et al.*, 2007; Bowen *et al.*, 2013), we still know little about the pre-Cenozoic fossil record of decapod crustaceans in low latitudes, limiting our understanding of the origins and evolution of tropical crab biotas through time (Luque *et al.*, 2017b).

Here we describe an exceptionally preserved crab from the early Late Cretaceous (Cenomanian–Turonian, ~95–90 Ma) of Colombia and USA, a chimaeric novel body form, and remarkably one of the most anatomically complete early crabs discovered to date (Figs 4.1–3). Despite its small size (~4–10 mm carapace width), its stunning degree of preservation reveals many features rarely seen in the crustacean fossil record, including sexually dimorphic pleopods, the first and second antennae, pediform mouthparts, and large compound eyes bearing facets and optical lobes.

Comparisons of †*Callichimaera* with living and fossil crabs revealed the group as a unique lineage of ancient brachyurans that evolved during a period of extensive morphological experimentation (Fig. 4.3), and the first crab lineage to evolve adaptations for active swimming. Our findings i) support the view that early brachyurans experienced a considerable versatility of form (Vermeij, 1973) during the Cretaceous, ii) hint at the evolution of novel forms via developmental processes such as heterochrony, iii) suggest that swimming paddles in crabs can be the result of exaptation of repurposed flattened limbs for digging in the sediment, and iv) demonstrate that the loss of a typical 'crab-like' body plan, or 'decarcinization' has occurred independently several times during the last 130 Ma among both false and true crabs (Fig. 4.4).

4.2. Materials and methods

4.2.1. Origin of specimens

The specimens from the type series were collected from carapace–rich, appendage–rich, and scattered remains surfaces, in the Cenomanian and Turonian (~95–90 Ma) Churivita Group of Colombia, and Frontier Formation of USA, between 2005 and 2014, and are deposited in the paleontological collections at the Colombian Geological Survey (Bogotá, Colombia), the Mapuka Museum of Universidad del Norte (Barranquilla, Colombia), and the Paleobiology collections at the National Muesum of Natural History, Washington D.C, USA. Due the very small size (microns) of some external and internal features, specimens preserving fine-detailed eyes were studied under Scanning Electron Microscope (SEM). Full geological and stratigraphic information is available in the Supporting Information at the end of this chapter.

4.2.2. Phylogenetic analyses

The dataset, containing 47 taxa and 86 adult morphological characters, was built in Mesquite 2.75, and analyzed under Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) methods. MP was performed in PAUP* 4.0b10, under a heuristic search analyses with random addition sequence and 1000 replications with random input order. Bootstrap and jackknife values were calculated in TNT 1.1, after 1000 iterations each. ML was performed in IQ-Tree v. 1.5.6, using the Mk model of morphological character evolution; node support was estimated using ultrafast bootstrap and SH-aLRT options with 1000 replicates each. BI was performed in MrBayes v. 3.2.6, under traditional Mk model with an ascertainment bias correction to account for scoring only variable morphological characters. Two independent runs with four chains each were run for 50 million generations. The relative burn-in fraction was set to 50% and the chains were sampled every 1000 generations. All characters were equally weighted and unordered. Full methods and any associated references are available in the Supporting Information at the end of this chapter.

4.3. Results

4.3.1. Systematic paleontology

This work and the nomenclatural acts it contains will be registered after publication in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature http://zoobank.org/xxxxx. The Zoobank Life Science Identifiers (LSIDs) for this publication are urn:lsid:zoobank.org:act: XXXXXX, urn:lsid:zoobank.org:act: XXXXXX, urn:lsid:zoobank.org:act: XXXXXX, and urn:lsid:zoobank.org:act: XXXXXX.

The data for this study are available in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.[NNNN], Morphobank http://www.morphobank.org/xxxxx, and TReeBASE (https://treebase.org/xxxxx).

Arthropoda von Siebold, 1848

Decapoda Latreille, 1802

Brachyura Latreille, 1802

†**Callichimaeroida** section nov.

Included superfamily. †Callichimaeroidea superfam. nov.

Diagnosis. As for type species.

†**Callichimaeroidea superfam**. nov.

Included family. †Callichimaeridae fam. nov.

Diagnosis. As for type species.

†**Callichimaeridae** fam. nov.

Included Genus. †*Callichimaera* gen. nov.

Diagnosis. As for type species.

†***Callichimaera*** gen. nov.

Included species. †*Callichimaera perplexa* sp. nov. by monotypy and original designation.

Diagnosis. As for type species.

†***Callichimaera perplexa*** gen. et sp. nov.

Fig. 4.1, Supporting Figs S4.4–S4.6

Diagnosis. Small crab (<10 mm carapace width, <16 mm carapace length) with carapace longer than wide, fusiform; with distinct cervical and branchiocardiac grooves; bearing axial longitudinal ridge and postfrontal ridges. Sternites 1 to 4 visible ventrally; sternites 4 to 7 unfused, with sutures distinct, and axially sulcate by linea media; all sternites are unique in shape and size; sternite 5 very wide; suture 5/6 complete, irregular, sinuous; lacking true sterno–pleonal cavity; thoracic gonopores not recognized in males or females; female spermatheca paired in sternite 7, positioned posterior to coxa of pereiopod 3. Pleon symmetrical, sexually dimorphic, narrower in males than females, and in both sexes narrower than sternite 6. Pleonal somites not fused, lacking articulated rings and uropods, bearing dorsal median tubercle; pleonites 1 to 3 exposed sub-dorsally; lacking pleonal, sternal, or appendicular locking mechanisms. Rostrum bifid; first and second antennae short, between the eyes; eyes very large, cornea strongly dilated and sub-globular, bearing short ocular peduncles; lacking orbits, orbital fissures, or any protective structure; third maxillipeds (mxp3) pediform, elongate, with 'crista dentata', length of ischium + merus slightly longer than length of palp, merus positioned far back from anterior of carapace or basal antennal segments. Chelipeds (claws) isochelous, manus stout, and fixed finger deflected ~90˚; pereiopods (legs P2–P3) large and wide, with propodus and dactylus flattened, paddle-like; P4–P5 short and narrow, with dorsal longitudinal keel, lacking spines, not sub-chelate or modified to carry objects, neither flattened nor paddle–like; P5 smallest, well developed but reduced, carried sub-dorsally.

Description. Dorsal carapace: Small, elongate, fusiform, longitudinally sub–ovate in outline, with maximum width two–thirds maximum length of carapace, widest at posterior two–fifths carapace length at level of sternite 5; cervical groove distinct, well developed, ending at anterolateral margin, shallow antero–distally and more pronounced mesially, interrupted axially by a short mesial longitudinal ridge; branchiocardiac groove distinct, shallow at middle portion of carapace, more pronounced toward the anterolateral margin; dorsal carapace finely granulated; two short, parallel postrostral ridges arise at base of rostrum and deflect posterodistally, apparently continuing longitudinally as pre–cervical ridges separating the protogastric and mesogastric regions; longitudinal axial ridge prominent, more or less continuous, extending from mesogastric region, beginning approximately at first anterior quarter of carapace length and extending to cardio–intestinal region, interrupting the cervical groove axially and bearing a row of few low–relief tubercles along its length; unornamented lateral branchial ridges present (Fig. 4.1A–B; Supplementary Fig. S4.5A–B, D). Rostrum longer than wide, bifid, sub-square, with sides almost parallel, depressed axially, broader at the base, representing one–tenth the maximum carapace length; fronto–orbital margin short, about one–third maximum carapace length; absence of true orbits, augenrest, and orbital fissures, bearing only one short, blunt spine–like protuberance at mid-orbit. Anterolateral margin sinuous, poorly defined, bearing one short, blunt spine–like protuberance at end; posterolateral margin convex at middle portion of carapace and straight posteriorly; posterior margin concave, slightly less than half the maximum carapace width.

Ventral Carapace: Thoracic sternum wide anteriorly, narrow posteriorly; sternites 1 to 4 forming an elongated sternal crown (Fig. 4.1d–f; Supplementary Fig. S4.4A–D); sternites 1 to 3 distinct, fused, forming a triangle, with straight, convergent anterolateral margins, nearly as long as sternite 4; sutures 1/2 and 2/3 not clear; sternite 4 sub–quadrate, slightly wider than long, width one–fourth carapace width, length one–eighth carapace length, not mesially depressed or furrowed, lateral margins smoothly concave, anterior portion nearly equal to posterior, strongly concave posterior margin mesially; suture 3/4 distinct only laterally; sternite 5 the broadest sternite, maximum width anteriorly, more than two–thirds maximum carapace width, maximum length near sternum axis, one–fourth the maximum carapace length, depressed mesially by linea media, with lateral margins straight, convergent posteriorly, and bearing long and prominent longitudinal ridge on each side, which extend along position of maximum length, parallel to main axis; suture 4/5 complete, rather well defined by a deep sinuous groove, with anterior mesial portion of sternite 5 articulating into sternite 4 posterior margin concavity (Fig. 4.1D–F; Supplementary Fig. S4.4A–B); sternite 6 very different in shape outline and in size from sternites 5 and 7, maximum width at anterior portion, approximately half maximum carapace width, maximum length approximately one–sixth carapace length, strongly depressed mesially by a deep cleft, occasionally bearing a subtle ridge on each side, almost parallel to main axis, with anterior margin irregular, extending obliquely posteriorly from main axis, producing a sinuous concavity posteriorly near where sternite 5 longitudinal ridge ends (Fig. 4.1D, F; Supplementary Fig. S4.4A–D), and describing a convex, arcuate loop ending at lateral margin, which is straight, converging posteriorly, suture 5/6 complete, well defined by a deep groove; sternite 7 reduced, different in shape and size from sternites 5 and 6, maximum width at posterior portion, nearly parallel to carapace posterior margin, approximately one–sixth maximum carapace width, maximum length near carapace axis, approximately one–seventh carapace maximum length, inverted V–shaped, strongly depressed mesially, with margins diverging posteriorly, suture 6/7 complete, well defined by a deep groove; sternite 7 in one female specimen bearing a paired spermatheca axially (Fig. 4.1H; Supplementary Fig. S4.6H); sternite 8 not seen. Thoracic gonopores not present in males or females.

Pleon: Symmetrical, short, lacking articulated rings and uropodal plates, sexually dimorphic. Female pleonites sub–rectangular in outline, pleonite 1 to 3 exposed dorsally, pleonite 1 reduced, pleonites 2 to 5 similar in shape and size, epimeres with a longitudinal depression, separated from the tergum; each pleonite bearing dorsal axial tubercle that may be distinctly spiniform in small specimens; in one specimen (Supplementary Fig. S4.5C), pleonal somite 4 tergum bearing a notch, extending anterolaterally to postero–mesial portion; pleonites and telson preserved in a few specimens (Supplementary Fig. S4.6G–H), pleonite 5 similar in shape to pleonites 2–4 but smaller; pleonite 6 with a concave posterior margin articulating with telson; telson short, wider than long, strongly convex anteriorly. Female pleopods 2–5 present, small, slender, similar in shape and size (Supplementary Fig. 4.S6E–F). Male pleonites narrower than females, pleonite 6 and telson exposed ventrally in one male specimen (Supplementary Fig. S4.6A–C); pleonite 6 longer than wide, semi–rectangular in outline, posteriorly arcuate, concave, articulating with telson; telson small, lanceolate, longer than wide, approximately two–

thirds as long as pleonite 6 length. Male first two pairs of pleopods (gonopods) slender and slightly arched, highly sclerotized (Supplementary Fig. S4.6A–C); pleopods 3–5 absent.

Eyes: Very large (each nearly 15% the length of carapace, or 25% the width of carapace), approximately as long as wide, round to semi–ovate in outline, always exposed and lacking any protective structure; compound eye facets predominantly hexagonal and in hexagonal arrangements through most of the outer–middle portion (Fig. 4.1J–M); three retinal layers are recognizable in one specimen (Fig. 4.1M); eyestalk short and stout, one–third the length of eye.

Cephalic appendages: first and second antennae (antennula and antenna s.s., respectively) short and slender, between the eyes, antenna as long as eye maximum length, first segment broad, one–fourth the length of rostrum (Fig. 4.1J, L).

Oral appendages: Third maxillipeds pediform, articulating with postero–distal portion of sternite 3; endognath ischium elongate, semi–rectangular in outline, as long as sternite 4 width, two–fifths as wide as long, bearing a crista dentata armored with four to five small, acute, evenly spaced spines on internal margin; merus elongate, semi–quadrate in outline, slender, somewhat shorter than ischium, more than twice as long as broad; palp (carpus–dactylus) slightly shorter than ischium + merus, directed forward; merus of endognath never reaching anterior carapace, ischium + merus length approximately one–fifth carapace maximum length; exognath slender, nearly as long as endognath ischium, as wide as one–third endognath ischium width, with nearly straight outer margin; endognath of second maxilliped very small, pediform; mandibulae as long as half the endognath ischium length, robust, slightly asymmetrical in shape, but similar in size, left mandible describing a concave curvature on occlusal surface slightly different from the right mandible (Supplementary Fig. S4.4E).

Pereiopods: Chelipeds (P1) isochelous, ischio–merus semi–rectangular, about one–fourth as long as carapace length; carpus sub–trapezoidal, as long as two–thirds the length of merus; propodus–carpus articulation subparallel to merus long axis; propodus height as long as ischio–merus length, with a blunt tooth–like projection at outer distal corner, close to articulation with dactylus; manus stout and inflated, about two times carpus width, often tuberculate; pollex three times longer than carpus, broad, deflected ~90° with respect to propodus length axis, with 10 to 15 small, sharp, and irregular, well–developed denticles on occlusal surface, and distal denticle upturned; dactylus slender, with distal denticle downturned, slightly shorter than fixed finger, smooth edentulous occlusal surface, except for occasional one or two small, fine denticles near junction with propodus (Fig. 4.1C, H; Supplementary Fig. S4.4A, B). Pereiopod 2 (P2) the longest of all pereiopods, usually as long as, or slightly longer than, maximum carapace length; coxa semi–rectangular in outline, long, articulating laterally with sternite 5; basis poorly defined, apparently small, with a slender condyle that articulates with coxa; ischio–merus subrectangular, slightly convex forward, bearing a small spine at upper distal margin, close to articulation with carpus; carpus length one–third the length of ischio–merus, trapezoidal in outline, narrow at articulation with merus, may bear small spines on outer margin; propodus elongate, ovoid, twice the length of carpus, or two–thirds as long as ischio–merus length, may be serrated, sometimes with one to three small, acute, spiniform projections at anterior edge close to articulation with dactylus, narrow at articulation with carpus; dactylus broadly lanceolate, as long as propodus, narrow at articulation with propodus (Fig. 4.1B, D, G–I; Supplementary Figs S4.4A, C, S4.5C–E, S4.6A); P2 segments bearing a fine rim of evenly spaced setal pits; P3 almost identical in shape and size to P2, but slightly shorter, coxa articulating laterally with sternite 6, and bearing a small, slender and acute posterior coxal spine. Pereiopods 4 to 5 similar in shape and very different in shape and size from P2–P3 (Fig. 4.1D, H–I, N; Supplementary Figs S4.4A, C, S4.5C, E); P4 slender, half the length of P2–P3, with a median carina along all sclerites; ischio–merus subrectangular, often finely granulated, broader posteriorly; carpus half the size of ischio–merus, subquadrate, narrow at articulation with merus; propodus subrectangular, one–third longer than carpus length, and similar in size to ischio–merus; dactylus sharp, slender and acute, similar in length to propodus, but two–thirds the width, weakly serrate, narrow at articulation with propodus. Pereiopod 5 the smallest pereiopod, one–third length of P3, slender, with median carina along all the segments, similar in shape to P4 but considerably smaller and carried subdorsally; coxae and basi not recognized; ischio–merus fused, sub–perpendicular to main carapace axis, as long as P4 dactylus; carpus length half the ischio–merus length, narrow at junction with ischio–merus; propodus as long as ischio–merus length, narrow at junction with carpus; dactylus slender and acute, as long as propodus.

Etymology. The section, superfamily, family, and generic names are derived from the Greek prefix calli- ‘*kalos*’ (beautiful), alluding to its exceptional preservation, and *Chimaera*, the fabulous mythological beast commonly represented as composed of parts of different animals such as lion, goat, and snake, alluding to its startling combination of traits present in separate higher decapod taxa, e.g., eubrachyurans, podotreme brachyurans, anomurans, and some macrurans. The trivial name derives from the Latin '*perplexus*', referring to its puzzling anatomy and phylogenetic affinities. Gender feminine.

Holotype. IGM p881215, specimen preserved in ventral view (Fig. 4.1D–F), deposited in the paleontological collections of the Colombian Geological Survey, Diagonal 53 #34 – 53, Bogotá D.C., Colombia. Carapace length: 8.5 mm, carapace width: 5.2 mm.

Additional material. Paratypes IGM p881184 to IGM p881214, and IGM p881216 to IGM p881221, deposited in the paleontological collections of the Colombian Geological Survey; paratypes MUN–STRI 27044–01 to MUN-STRI 27044–010, MUN–STRI 27045–01 to MUN-STRI 27045–020, deposited in the Mapuka Museum of Universidad del Norte, Barranquilla, Colombia; paratypes CIP XXXX-XXXX, deposited in the Centro de Investigaciones Palentológicas (CIP), Villa de Leyva, Boyacá, Colombia. Paratypes USNM 605049 to USNM 605056, deposited in the Paleobiology collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States.

Measurements. Range of measurements: holotype carapace length: 8.5 mm, carapace width: 5.2 mm; smallest paratype IGM p881220: carapace length: 6.6 mm, carapace width: 3.8 mm; largest paratype MUN-STRI 27045–015: carapace length: 15.1 mm, carapace width: 9.6 mm.

Type locality and horizon. Upper Churuvita Formation, upper Cenomanian–lower Turonian (~95–90 Ma), Pesca, Boyacá, Colombia (Supporting Figs S4.1–S4.2), from carapace-rich and appendage-rich surfaces. Other paratypes: Frontier Formation, lower–middle Turonian (~90 Ma), Wyoming, United States.

Systematic remarks. †Callichimaeroida section nov. is placed within Decapoda Brachyura based on several characters: i) short first and second antenna between the eyes, ii) symmetric and sexually dimorphic pleon, iii) absence of articulating rings between pleonites, iv) reduced telson, v) absence of uropods or uropodal plates, vi) presence of modified male pleopods 1–2 as highly sclerotized gonopods, but missing pleopods 3–5, while the female bears pleopods 2–5, vi) third maxilliped with well–defined ischium and merus, vii) presence of only one pair of chelae or claws (pereiopod 1) thus pereiopods 2–5 achelate, and viii) P5 well developed, clearly visible in dorsal view, and neither sub-chelate nor modified for carrying or grasping (Fig. 4.1; Supporting Materials; Supporting Figs S4.4–S4.7). However, a precise phylogenetic placement of †*Callichimaera* within Brachyura is problematic because of its ‘chimaeric’ nature, the unknown molting linea, and possession of multiple distinctive characters typical of several fossil and extant Brachyura and Anomura clades (Figs 4.2, 4.4), but not collectively seen in any one taxon. These characters include: a lobster/raninid-like elongate carapace appearance, the pediform maxillipeds with a crista dentata, the spanner-like chelipeds, the large paddle–like P2-P3 legs, a symmetrical pleon lacking uropods or uropodal plates, the dissimilar shape and size of its sternites, and the large eyes lacking true orbits and orbital fissures (see Supporting Information).

†*Callichimaera* lacks the typical ‘crab-like’ body plan characterized by a shortening of the carapace, the development of well-defined lateral margins, and the ventral concealment of the pleon (Scholtz, 2014). The evolution of a crab-like body plan (=carcinization) has occurred independently at least four times among anomurans (e.g., in Aeglidae, Porcellanidae or porcelain crabs, Lithodidae or king crabs, and in some Paguridae or hermit crabs (Borradaile, 1916; Cunningham *et al.*, 1992; McLaughlin and Lemaitre, 1997; Hiller *et al.*, 2010; Tsang *et al.*, 2011; Anker and Paulay, 2013; Bracken-Grissom *et al.*, 2013), and multiple times among brachyuran crabs (e.g., in Dromioidea, Eubrachyura), although carcinization has likely occurred in most podotreme groups independently (Fig. 4.3). However, some lineages have ‘decarcinized’ or lost the crab-like body form (Scholtz, 2014), typically associated with the evolution of fossoriality in groups like masked crabs (Eubrachyura: Corystoidea), mole crabs (Anomura: Hippoidea) and frog crabs (Brachyura: Raninoidea) (Bellwood, 2002) (Fig. 4.4). Although the fossil record of mole crabs is sparse and fragmentary, the exceptional fossil record of stem and crown raninoidans – ranging from Early Cretaceous to present – allows the direction of change of key morphological traits in the transition from a carcinized to a decarcinized body to be investigated. For example, during the Early Cretaceous, as the carapace of some stem-group raninoidans lengthened and their thoracic sternum narrowed (i.e., Palaeocorystidae), sternites 5

to 8 narrowed axially and with them the arthrodial cavities for their pereiopods (Luque, 2015a), while the sternites 7–8 and the associated coxae of P4 and P5 migrated towards a more postero-dorsal plane, thus forcing the pleon to unfold backwards (Luque *et al.*, 2012; van Bakel *et al.*, 2012a; Karasawa *et al.*, 2014; Luque, 2015a). By the end of the Early Cretaceous, both Palaeocorystidae and crown-group Raninoidea (Fig. 4.3) had already evolved flattened pereiopods for back-burrowing and legs with a ~90 degree angle of articulation between the merus and carpus (Fig. 4.4), but only Raninoidea had narrow branchiostegites and exposed pleurites bridging their narrow posterior dorsal and ventral carapaces (Bourne, 1922; van Bakel *et al.*, 2012a; van Bakel, 2013). Thus, the 'naked' pleurites, or 'gymopleura', is a synapomorphy exclusive of the crown–group Raninoidea due to their strong decarcinization, not seen in other raninoidans including Palaeocorystoidea, and must have evolved during the late Early Cretaceous at the latest (van Bakel, 2013).

The superficial resemblance of †*Callichimaera* to other decarcinized crabs, particularly raninoids and palaeocorystids, might initially suggest a fossorial lifestyle. Some of the advantages of a fossorial habit include avoiding visual detection by predators and prey, and facilitation of ambush predation from concealed positions (Stevcic, 1973; Luque, pers. obs. in *Raninoides benedicti*). But several traits of †*Callichimaera* are unlike any other decarcinized crabs, and indicate that they were not specific adaptations for burrowing or burying but more likely for efficient swimming. First, sternites 5–6 are very broad — nearly as wide as the carapace — and must have housed large thoracic muscles to control the large paddle-like legs P2–P3 (Figs 4.1–4.2; Supporting Figs S4.4–S4.7). These legs also lack the ~90 degree angle of articulation between the carpus and merus seen in typical decarcinized crabs, which would prevent the distal segments from moving near the carapace to aid in back-burrowing (Fig. 4). Also, legs P2 and P3 have articles with margins lined by setal pits where setae insert. Setae along these paddle-like legs would have increased the surface of the paddles, such as in blue crabs and munnopsid isopods, where they aid in the sculling stroke. In addition, legs P4 and P5 differ markedly from legs P2 and P3; they are reduced, narrow, axially keeled, and directed dorso-posteriorly (Fig. 4.1), and so would be of little use for digging. In hippoids and raninoids, leg P4 is usually similar in shape to the preceding legs (P2 and P3), but leg P5 is reduced and not visible dorsally (hippoids), or exposed and modified for digging (raninoids) (Fig. 4.4).

Furthermore, †*Callichimaera* does not exhibit obvious respiratory adaptations seen in many extant fossorial crab species, such as accessory exostegal channels, or a sieving mechanism for water intake formed when chelipeds are tightly pressed ventrally against the subhepatic region, the pterygostome, and the buccal frame (Bellwood, 2002; van Bakel *et al.*, 2012a). In hippoids and corystoids (Fig. 4.4C, H–I), the setae along the large second antennae interlock to form a tube or 'snorkel' that filters and directs the water flow posteriorly; in mole crabs the second antennae also function in filter feeding. Furthermore, decarcinized burrowing crabs usually have spinose fronto-orbital and/or antero-lateral margins, have small eyes and slender eyestalks that retreat into orbits for protection, or even eyes so reduced that are barely exposed, as in *Symethis* (Fig. 4.4). †*Callichimaera* lacks these digging adaptations. Its eyes are unusually large, lacking orbits, and not protected by spines or any other structures, so they must have been permanently exposed even under times of stress or if buried.

Results of the Maximum Parsimony (MP) and Maximum Likelihood (ML) analyses largely agree on the arrangement of the ingroup taxa, including placement of †*Callichimaera* as an independent lineage branching off prior to the extinct †Torynommoida and †Etyoida (Supplementary Figs S4.7, S4.8). The Bayesian Inference (BI) consensus tree presents the least resolved topology with several major brachyuran lineages collapsed in a polytomy (Supplementary Fig. S4.9). Although BI has been shown to produce accurate topologies when dealing with morphological data (Wright and Hillis, 2014; O'Reilly *et al.*, 2016), it remains very sensitive to the consistency of the phylogenetic signal present in the data set, selection of priors, and heterogeneity of evolutionary rates across different lineages on a tree. Since BI uses marginal likelihoods to select optimal topology (as opposed to the joined likelihood in the ML estimation), it is more sensitive to inconsistencies in a data set. The lack of resolution in our BI consensus topology is best explained by multiple cases of convergent traits and disparity in evolutionary rates (paedomorphosis, high phenotypic plasticity, etc.) across lineages.

4.4. Discussion

4.4.1. Heterochronous development of the chimaeric body plan

The versatility of the 'crustacean' body form is strongly regulated by Hox genes (Averof and Patel, 1997; Schram and Koenemann, 2004; Martin *et al.*, 2016) and modeled by the interplay of development, environment, and ecology (Jablonski, 2005; Wolfe, 2017). Heterochrony, or changes in developmental timing and/or rates, have played an important role in the evolution of novel forms and functions (Jablonski, 2005; Haug and Haug, 2016), and paedomorphosis, i.e., the retention of juvenile or even larval traits into adulthood, has contributed to the evolution of disparate anatomies in eucrustaceans (Newman, 1983; Schram, 1986). The anatomical character richness seen in *Callichimaera*, the large sample size (n=64) and size ranges (body width 3.8–9.6 mm, body length 6.6–15.1 mm), its presence in localities of Colombia and USA, and its exquisite preservation, provide us with a unique opportunity to study aspects of its growth, development, and functional morphology, and examine the role of development on the evolution of novel crab forms during the Cretaceous.

†*Callichimaera* superficially resembles a larval stage known as a megalopa: the transitional (final) larval stage between the swimming planktonic zoea larva and the first benthic juvenile crab stage (Wolfe, 2017). Since megalopae are mostly a single larval stage, they tend to vary minimally in size and shape among conspecifics (Martin, 2014). The only fossil crab larvae currently known are one megalopa from the Late Jurassic Solnhofen lithographic limestones in Germany (~150 Ma) (carapace span ~5 mm) (Haug *et al.*, 2015), and a couple of minute Early Cretaceous zoea from the fossiliferous Santana Group in Brazil (~110 Ma) preserved in fish stomach contents (carapace span >2 mm) (Maisey and Carvalho, 1995; Luque, 2015a). †*Callichimaera* is clearly not a zoea stage. However, it does share characteristics of some crab megalopae, like its general carapace shape or habitus, the apparent lack of a clear molting linea, the sub-dorsal extension of the pleon, the leg-like maxillipeds armed with spines, and its large unprotected and unconcealed eyes lacking orbits.

However, †*Callichimaera* differs from a megalopa larva in several important ways. First, it exhibits a range of body sizes (6.6 to 15.1 mm carapace length, 3.8 to 9.6 mm carapace width, see *SI Appendix*), consistent with several growth instars. Second, brachyuran megalopae have uropods or relicts of them, and are not sexually mature, thus lack extreme sexual dimorphism (Martin, 2014). †*Callichimaera*, on the contrary, lacks any trace of uropods, and displays clear sexual dimorphism in both the pleon and pleopods in larger specimens; males bear a pair of well-developed sclerotized gonopods 1–2 but lack pleopods 3–5, and females bear unmodified pleopods 1–5 (Supporting Information, Fig. S6). Finally, †*Callichimaera* has distinctive chelae that are more typical of juvenile/adult crabs like some frog crabs and †*Retroscichela* (Feldmann *et al.*, 1993) than megalopa larvae (Martin, 2014). Thus, we conclude that the megalopa-like anatomy of adult †*Callichimaera* most likely originated via heterochronous development during early ontogenetic stages (Vermeij, 2015), and the early fixation of some juvenile traits in adulthood via paedomorphosis (Martin *et al.*, 2014) (Supporting Information).

4.4.2. Convergence of paddle limbs in aquatic euarthropods

The peculiar oar-like pereiopods P2 and P3 of †*Callichimaera* are convergent with swimming/digging limbs of other euarthropods, such as the 6th prosomal appendages of some eurypterids (sea scorpions), the 2nd and 3rd thoracic legs of gyrinid beetles (whirligig beetles), the 5th to 7th pereiopods of deep-sea swimming munnopsid isopods, the 4th pereiopod of extinct cenomanocarcinid crabs, and 5th pereiopod of portunids (swimming blue crabs) (Plotnick, 1985; Marshall and Diebel, 1999; Voise and Casas, 2009; Xu *et al.*, 2012; Luque, 2015a). Although most of these structures are not homologous — they arise from different body metameres and may involve different podomeres — are analogous as specialized multi-elemental modules suited for efficient swimming and/or digging. Curiously, after the disappearance of paddle-legged eurypterids by the late Permian around 250 Mya (Tetlie and Poschmann, 2008), no fossil arthropod to our knowledge had evolved such highly modified thoracic limbs until the evolution of †*Callichimaera* more than 95 Mya. The absence of other aquatic arthropods with extremely enlarged, flattened, and uniramous swimming legs from deposits spanning this 150-million year gap remains puzzling.

Swimming in most adult decapod crustaceans, such as shrimps and lobsters, is achieved via paddling with biramous pleopods, and/or the flexion of their muscular pleon and caudal fan. The loss of a muscular pleon in the ancestors of crabs, and the reduction of the pleon, pleopods, and caudal fan in most groups, preclude them from active swimming in the same way. Instead, highly specialized groups like swimming crabs (Eubrachyura: Portunoidea) and moon crabs (Eubrachyura: Matutidae), have evolved modified podomeres in one or more legs for digging, swimming, or both (Hartnoll, 1971b; Števčić, 1983; Bellwood, 2002). The long, flattened oar-like legs P2 and P3 of †*Callichimaera* resemble the spatulate legs of some moon crabs, but differ from other swimming and digging crabs in the lack of oval-shaped, leaf-like, or scythe-like distal podomeres, and the nearly 90 degree angles formed between the meri and carpi podomeres

(Fig. 4.4A–C, F–G). Highly modified paddle- and shovel-like legs have evolved independently at least seven times in crabs, shaped by similar lifestyles, resulting in striking convergence of forms and functions (Fig. 4.4). Paleontological and neontological information suggest that swimming via paddle-like legs in brachyurans has evolved several times via exaptation from flattened shovel-like legs used for digging, into paddles for active swimming (Morris, 1993). †*Callichimaera* appears to be structurally suited for active demersal/pelagic swimming, although could have also been a facultative back-burrower, as seen in extant pelagic swimming crabs like *Euphylax dovii* or *Charybdis smithii* (Norse and Fox-Norse, 1977; Romanov *et al.*, 2009).

4.4.3. Phylogenetic and evolutionary implications.

†*Callichimaera perplexa* blurs the boundaries of how a 'crab' is defined. Both anomurans and brachyurans are generally thought to have evolved crab-like body forms from weakly- or uncarcinized ancestors. However, we show that a decarcinized body (loss of crab-like form) (Scholtz, 2014) is a recurrent phenomenon among both false and true crabs, and it has occurred independently at least five times since the Early Cretaceous or before (Figs 3, 4). It seems like †*Callichimaera* is a unique example of a decarcinized crab that seems well suited for active demersal/pelagic swimming instead of benthic fossorial habits, as indicated by the large unprotected eyes, the keeled fusiform body, and long frontal paddle limbs attached to large sternites. Although no other callichimaeroid taxa have been discovered beyond the putatively calichimaeroid-like †*Retrorsichela* (Supporting Information), an actively swimming †*Callichimaera* may have evolved from a distant fossorial ancestor, as it seems the case for several extant swimming crabs like portunids. The presence of coeval †*C. perplexa* fossils in localities of Colombia and USA, more than 4,000 km apart (Supporting Information, Fig. S1), suggests that a number of its mosaic characters — so disparate with respect to other adult decapod crustaceans — and the repurposing of flattened limbs for swimming, must have stabilized by the late Cenomanian–early Turonian about 95–90 Mya.

Based on our MP, ML, and BI results (Supplementary Figs S4.7–S4.9), plus those from several recent works on larval, foregut, fossil and extant adult morphology, and molecular data (Ahyong *et al.*, 2007; Brösing *et al.*, 2007; Scholtz and McLay, 2009; Karasawa *et al.*, 2011; Tsang *et al.*, 2014; Vehof *et al.*, 2018), we conclude that the podotreme brachyurans (i.e., where males and females have sexual openings at the base of the legs) do not form a natural group but rather a grade, with Dromiacea (= Homolodromioidea, Dromioidea, and extinct relatives) and Homoloida being the less inclusive clades, and the podotreme Raninoida, Cyclodorippoida, and extinct relatives are sequential sister groups of Eubrachyura (Fig. 4.3, Supplementary Figs S4.7–S4.9). The podotreme condition is plesiomorphic for decapod crustaceans, as it occurs in shrimps, lobsters, anomurans, and all brachyuran clades except for thoracotreme and female heterotreme Eubrachyura (Scholtz and McLay, 2009). Extinct clades like Dakoticancroida also appear to be closer to some eubrachyurans (e.g., Componocancroidea, Dorippoidea) than to less inclusive podotreme brachyurans (i.e. Dromiacea and Homoloida). Alternatively, the presence of spermatheca in podotreme crabs may have valuable phylogenetic implications and support a monophyletic Podotremata (Guinot *et al.*, 2013; Davie *et al.*, 2015b), but whether this or other sexual characters were gained/lost several times within total-group Brachyura remains unknown (Vehof *et al.*, 2018).

Regardless of tree topology, the enigmatic †*Callichimaera* seems to occupy an intermediate position between the earliest podotreme brachyurans and more derived podotremes plus Eubrachyura (Fig. 3, Supporting Information, Figs S7–S10), filling a major gap in the evolutionary history of true crabs. †*Callichimaera* might possibly be neither brachyuran nor anomuran, but rather a member of its own infraorder †Callichimaeridea. However, our present results do not support this. †*Callichimaera* seems to represent a novel lineage of brachyurans that evolved when crabs were undergoing a major adaptive radiation that included extraordinary morphological experimentation, before settling into the more familiar body forms seen today.

Crab diversity exploded during the Cretaceous (~145 to 66 Ma), with nearly 80% of the higher clades first known from this period (Schweitzer and Feldmann, 2015) (Fig. 4.3). The tropics today hold much of the world’s biodiversity, and have acted as cradle and a museum of diversity by producing and accumulating species through time (Jablonski *et al.*, 2006; Marshall, 2006; Kiessling *et al.*, 2010; Bowen *et al.*, 2013). Thus, is not surprising that the fossil record from tropical settings would preserve snapshots of its past diversity. Recent discoveries from the Cretaceous of tropical and subtropical Americas include either the oldest, or one of the oldest fossil records for several higher taxa (Luque *et al.*, 2017) previously thought to have originated in higher latitudes (Schweitzer, 2001; Feldmann and Schweitzer, 2006) (Supporting Information). Although our understanding of the origins of several true crab lineages is far from settled, these findings provide starting alternative hypotheses about the early evolution of several crab groups, and suggest the tropics overall might have played a role on the origins and diversification for some groups since at least the Early Cretaceous (Luque *et al.*, 2017b).

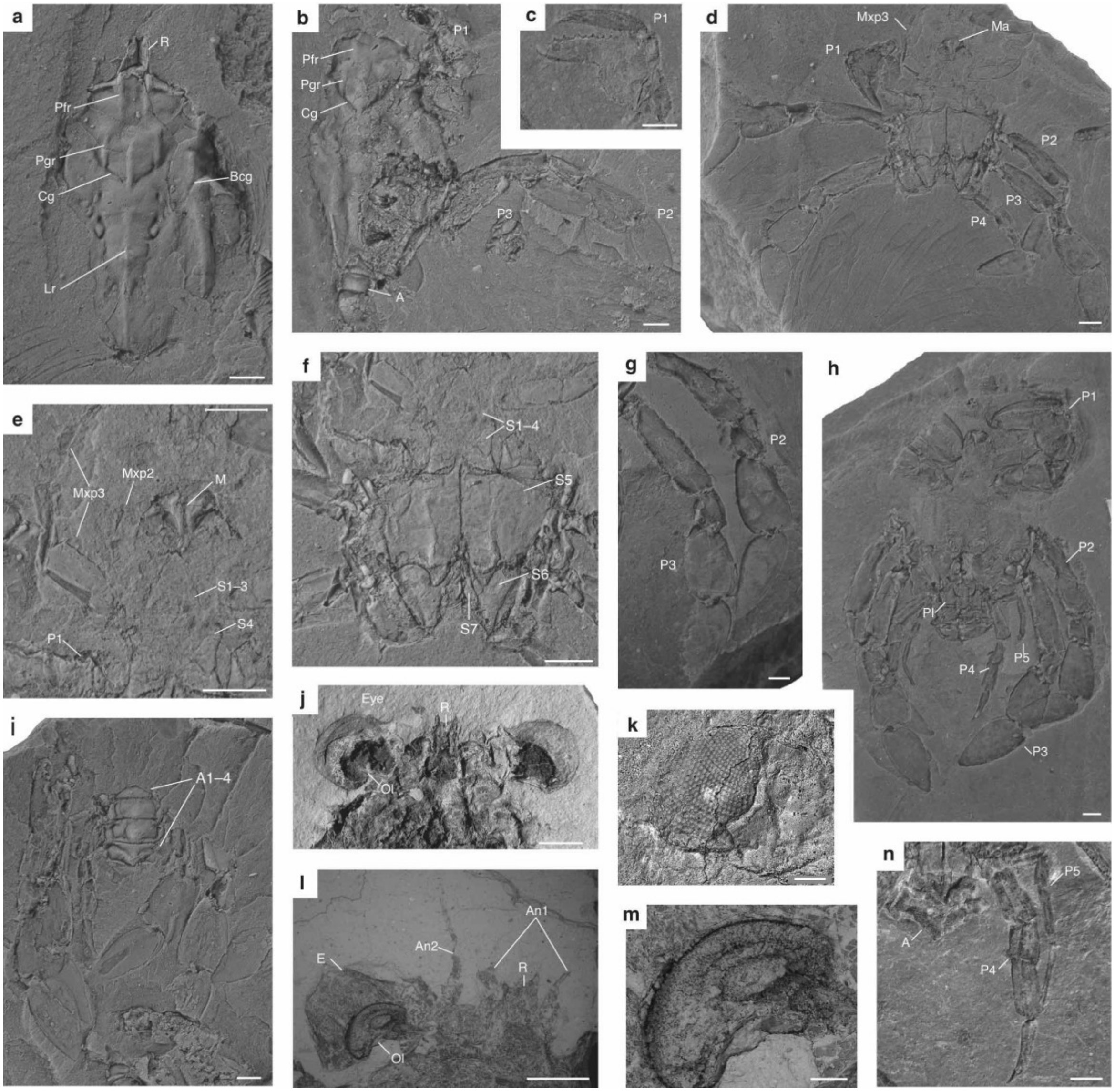


Figure 4.1. †*Callichimaera perplexa* n. gen. n. sp., lower Upper Cretaceous, Colombia. (a) Paratype IMG p881203, dorsal view. (b) Paratype IMG p881218, dorsal view. (c) Paratype IGM p881185. (d–f) Holotype IGM p881215: (d) ventral view. (e) Close–up of sternal crown and mouthparts. (f) Close–up of sternum. (g) Paratype IGM p881214. (h) Paratype IGM p881206, ventral view. (i) Paratype IMG p881217. (j) Paratype IGM p881208, showing the large eyes. (k) Paratype IGM p881220, SEM of eye preserving facets. (l–m) Paratype IGM p881209a: (l) SEM showing antennae, eye, and optical lobe. (m) Close-up of optical lobe. (n) pereiopods 4 and 5. Specimens coated with ammonium chloride. Abbreviations: A= pleon, A1–4= pleonites 1–4, An1= antenna 1 (antennula), An2= antenna 2, Bcg= branchio-cardiac groove, Cg= cervical groove, E= compound eye, Lr= longitudinal ridge, M= mandibula, mxp2= second maxilliped, mxp3= third maxilliped, Ol= optical lobe, P1= claw or cheliped, P2–P5= pereiopods 2 to 5, Pfr= post-frontal longitudinal ridge, Pgr= protogastric longitudinal ridge, R= rostrum, S1–7= sternites 1 to 7. Scale bars: (a–j), (l), (n), 1 mm; (k), (m), 200 µm.

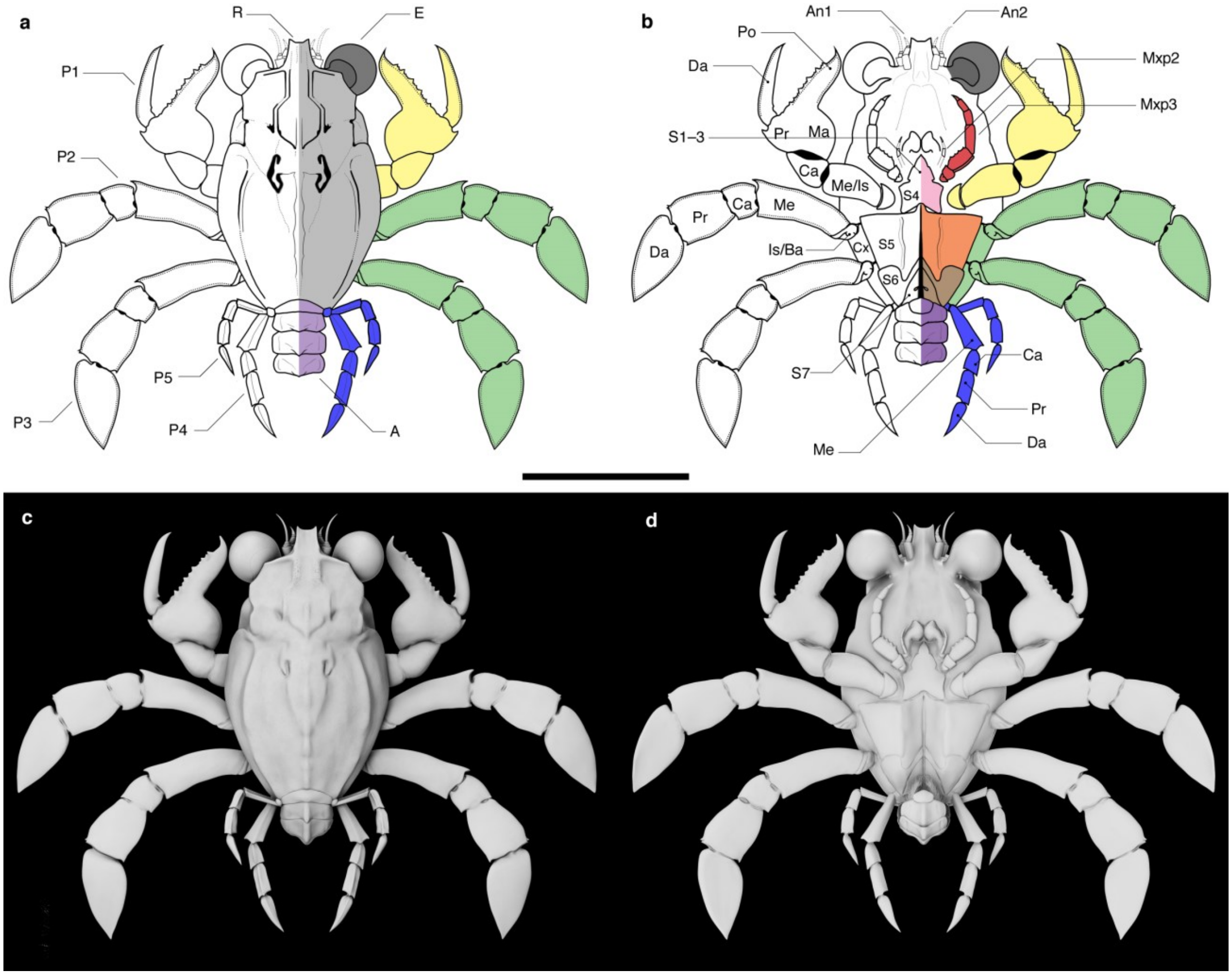


Figure 4.2. †*Callichimaera perplexa* n. gen. n. sp, reconstruction. (a–b) line drawing: (a) dorsal view. (b) ventral view. Colors indicate anatomical features convergent with other decapods: *light grey*- dorsal carapace, similar to some lobsters and †Palaeocorystidae (Brachyura: Raninoida); *dark grey*- large eyes, similar to †*Ekalakia* (Dromiacea: †Glaessneropsidae) and several homoloids; *red*- pediform mxp3 bearing a crista dentata, similar to lobsters, most anomurans, and early-branching brachyurans (Homolodromioidea, most Homoloidea); *yellow*- spanner–like P1, similar to Hippoidea, Raninoidea (Brachyura), and †*Retrorsichela*; *green*- flattened paddle–like legs P2–P3, similar to Matutidae (Brachyura: Eubrachyura); *blue*- reduced legs P4–P5, as in hermit crabs (Anomura: Paguroidea), podotreme brachyurans (e.g., Homolodromioidea, Cyclodorippoidea) and early-branching eubrachyurans (e.g., Dorippoidea); *orange*- sternites S5–S6 similar to †*Retrorsichela* and *Heikeopsis* (Eubrachyura: Dorippoidea); *purple*- symmetrical pleon lacks articulated rings and uropods/uropodal plates, as in most brachyurans. (c–d) digital reconstruction: (c) dorsal view. (d), ventral view. Abbreviations: A= pleon, An1= antenna 1 (antennula), An2= antenna 2, Ba= basis, Ca= carpus, Cx= coxa, Da= dactyl, E= compound eye, Is= ischium, Ma= manus, Me= merus, Mxp2–Mxp3= maxillipeds 2–3, P1= claw (cheliped), P2–P5= pereiopods 2–5, Po= pollex, Pr= propodus, R= rostrum, S1–7= sternites 1–7. Scale bar: 10 mm.

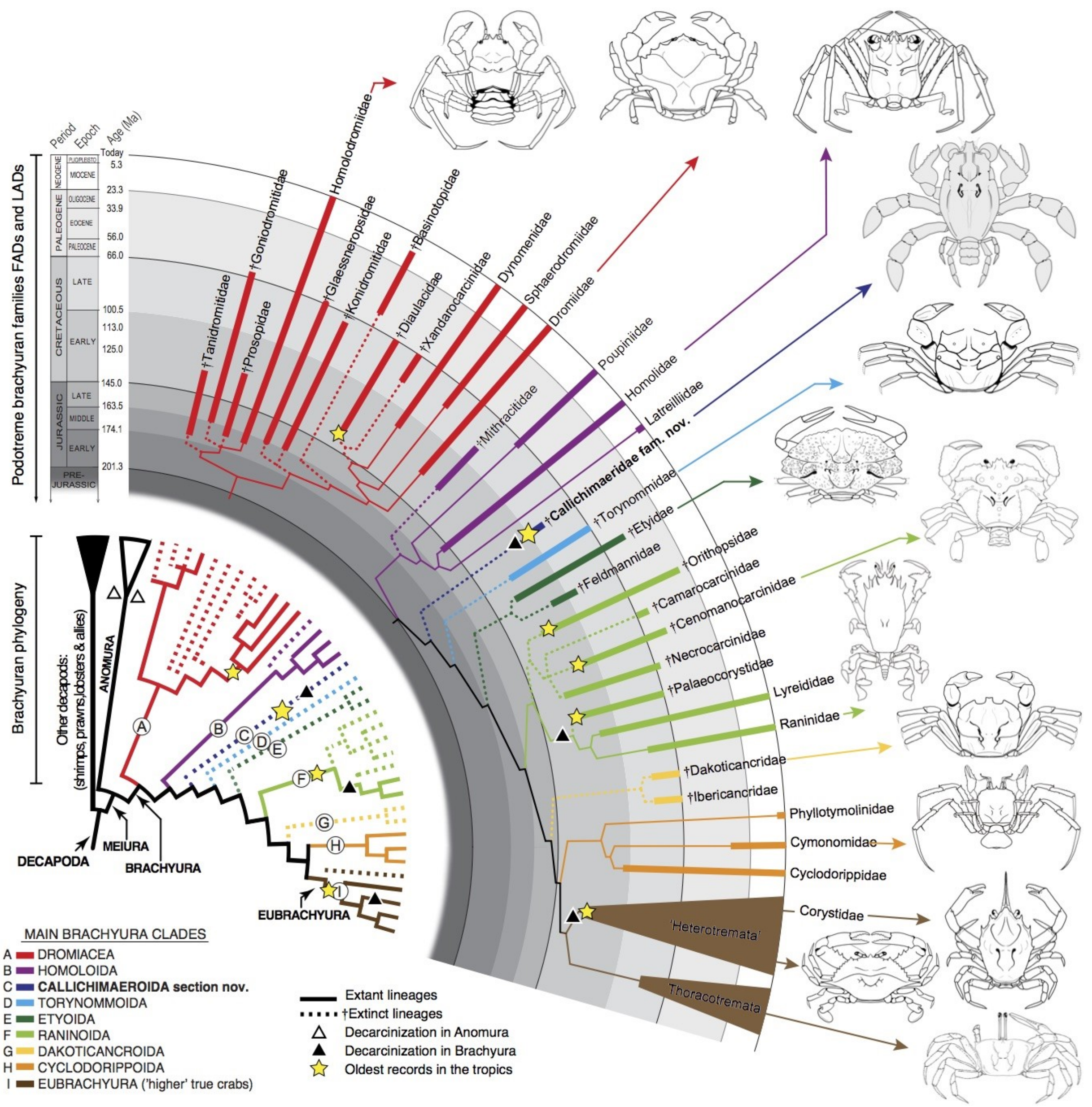


Figure 4.3. Phylogenetic relationships among the main families, superfamilies, and sections of 'true' crabs, or Brachyura. Tree topology after Supporting Figs. S6.7 and S6.8. Each color and letter in circle represents one of the nine major brachyuran evolutionary branches. Dromiacea (red, A) and Homoloida (purple, B) are first known from the Jurassic, while Callichimaeroida section nov. (dark blue, C), Torynommoida (light blue, D), Etyoida (dark green, E), Raninoida (light green, F), Dakoticancroida (yellow, G), Cyclodorippoida (orange, H), and Eubrachyura or 'higher' brachyurans (brown, I) are all first known from the Cretaceous. Thick solid lines represent the ages of the first and last occurrences of each family within the main clades. Dotted lines indicate extinct taxa; complete lines indicate living taxa. White triangles indicate that in Anomura, decarcinization has occurred twice (anomuran clades not illustrated). Black triangles indicate the three Brachyura lineages where decarcinization has occurred. Yellow stars indicate clades with their oldest records in tropical America.

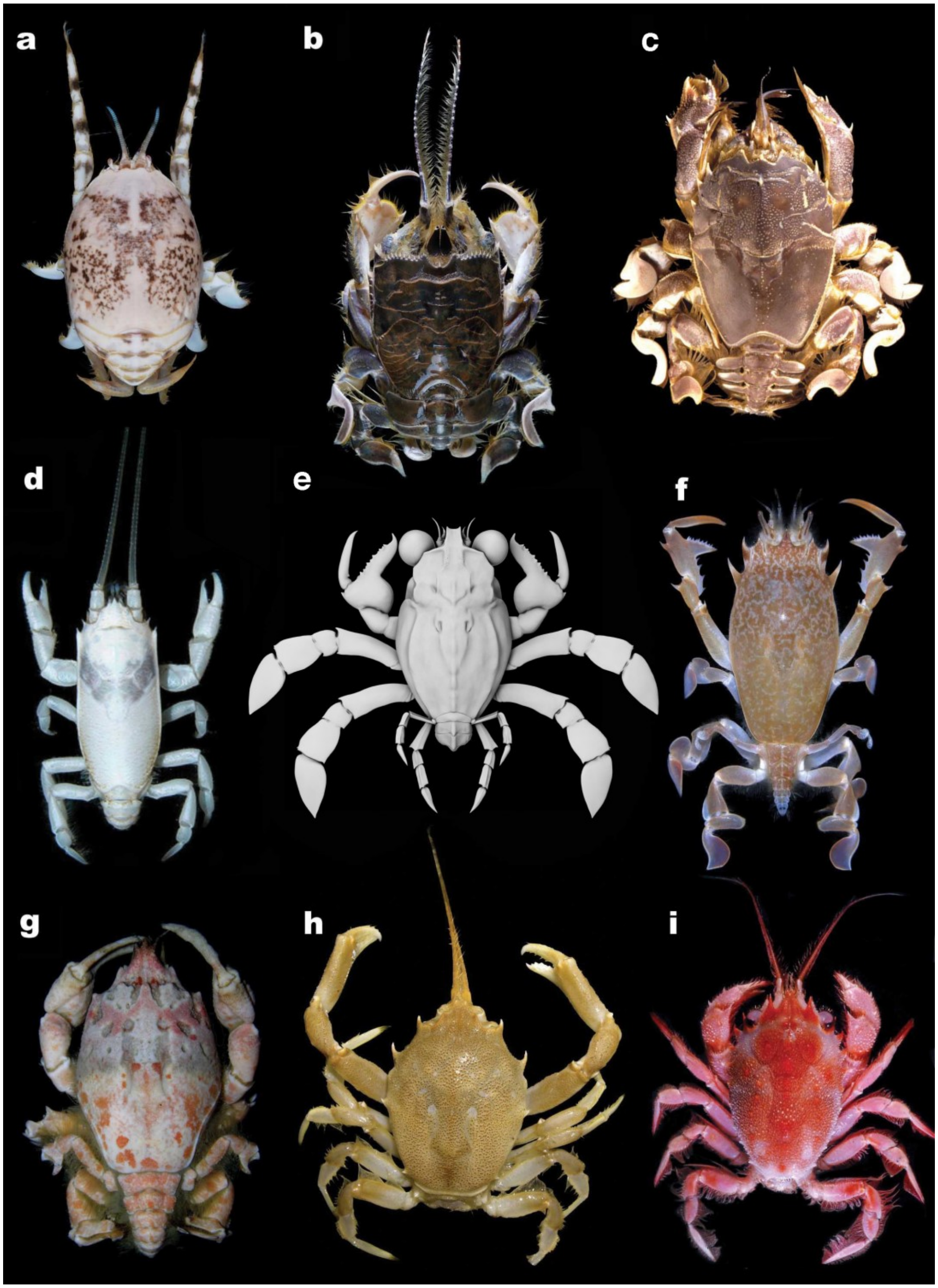


Figure 4.4. Convergent decarcinized body forms in various families of anomuran and brachyuran crabs. (a–d) Anomura: (a–c) Hippoidea: (a) Hippidae, *Hippa marmorata*, Taiwan (Photo by T.Y. Chan). (b) Albuneidae, *Albunea occulta*, Taiwan (Photo: T.Y. Chan). (c) Blepharipodidae, *Blepharipoda occidentalis* (photo: C. Boyko). (d) Galatheoidea, Porcellanidae, *Euceramus panatelus*, Panama (photo: A. Anker). (e–i) Brachyura: (e) †Callichimaeroidea, †Callichimaeridae, †*Callichimaera perplexa* n. gen. n. sp., Colombia and USA. (f–g), Raninoidea, Raninidae: (f) *Raninoides benedicti*, Panamá (photo: A. Anker). (g) *Symethis* sp. Panamá. (h–i) Eubrachyura, Corystoidea, Corystidae: (h) *Corystes cassivelaunus*, Belgium (photo: H. Hillewaert). (i) *Jonas distinctus*, Taiwan (Photo: T.Y. Chan).

4.5. Supporting Methods

4.5.1. Fossil specimens and preparation

The type series of †*Callichimaera perplexa* includes: holotype IGM p881215; paratypes IGM p881184 to IGM p881214, IGM p881216 to IGM p881221, deposited in the paleontological collections of the Colombian Geological Survey, Diagonal 53 #34 – 53, Bogotá D.C., Colombia; and paratypes MUN–STRI 27044–01 to MUN-STRI 27044–010, MUN–STRI 27045–01 to MUN-STRI 27045–020, deposited in the Mapuka Museum of Universidad del Norte, Barranquilla, Colombia. Paratypes USNM 605049 to USNM 605056, deposited in the Paleobiology collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States.

Specimens from the type series were collected from carapace–rich, appendage–rich, and scattered remains surfaces, and are generally compacted dorso–ventrally. However, the thoracic sternites, pleonites, dorsal carapaces, mandibles, and even internal optical structures are represented in three dimensions in some specimens. The specimens were exposed using fine tungsten carbide needles and pin vises, dissecting scalpel blades, and fine pneumatic pencils, under a Nikon Eclipse 80i microscope with camera lucida, and a Leica Macroscope with Spotflex digital camera. Broken or fragile samples were consolidated with the cyanoacrylate adhesive Paleo Bond™ PB40, and/or stabilized with Paraloid™ B72 and EtOH 95% as the solvent.

4.5.2. Microscopy, photography, measurement and illustration

Due to the very small size (microns) of some external and internal features, specimens preserving fine-detailed eyes were studied under Zeiss Scanning Electron Microscope (SEM) Evo 40vp under variable pressure, and Back-scattered Electron Detector (BSED) with acceleration voltages of 15 and 20kV. For optical photography, most specimens were coated with sublimated NH_4Cl prior to photographing, in order to enhance relief and fine ornament. Sets of photographs at different focal points were taken with a Nikon Eclipse 80i + Nikon Digital Camera Dxm 1200f, Olympus SZX16® Research Stereomicroscope with a digital camera Qimaging Retiga 2000R Fast 1394, Leica Macroscope with Spotflex digital camera, and/or a Nikon D3100 with MicroNikkor 60 mm lens. The resulting multi-layered stacks of photos were merged in a single high–definition image using the stacking software Helicon Focus. The photo editing was completed in Adobe® Photoshop CS5, and composite figure editing in Adobe® Illustrator CS5. For the morphological reconstructions of *Callichimaera*, we digitized camera lucida line drawings using a Wacom® Intuos4 Pen Tablet, whereas reconstructions and animations were performed using standard polygon and UV layout techniques in Autodesk Maya 2009. The structure, rendering, and topology of the base mesh were edited in Pixologic's Zbrush 4.0 for digital sculpting and high frequency detailing of the carapace.

4.5.3. Phylogenetic analysis

To assess the phylogenetic position of †*Callichimaera* among false and true crabs, we used a dataset modified from Karasawa *et al.* (2011), and incorporated new taxa and morphological information from additional works (e.g.,Feldmann *et al.*, 2008a; Luque *et al.*, 2012; van Bakel *et al.*, 2012a; Bracken-Grissom *et al.*, 2013; Guinot *et al.*, 2013; Karasawa *et al.*, 2014). Our modified data matrix incorporates 42 terminals: 5 outgroups (Astacidea, †*Platykotta*, *Galathea*, *Chirostylus*, and *Blepharipoda*) and 37 ingroups, including †*Callichimaera* (Supplementary Fig. 9; Supplementary Table 1; Supplementary Dataset S1). Some dromiacean taxa included in Karasawa *et al.* (2011), i.e., bucculentids, longodromitids, lecythocarids, as well as Viaiidae Artal *et al.*, 2012, and the family Paranecrocarcinidae Fraaije *et al.*, 2008; Schweitzer *et al.*, 2016, were excluded due to the high percentage of missing characters, which did not help resolve the topology. The resulting character–taxon matrix for 86 adult morphological traits (Supplementary Dataset S1) was constructed using the software Mesquite 2.75 Maddison and Maddison, 2007 [2011]. Undetermined or not preserved characters were scored as '?', and inapplicable characters as '–'. Multiple character states present in a single terminal taxon were scored as polymorphisms. Character scoring followed Brazeau (2011). Taxa in Supplementary Table 1 were scored in the matrix at the family level, to convey the morphological diversity seen among brachyuran clades and to examine the combination of plesiomorphic and apomorphic character states seen in *Callichimaera.* The final data set was analyzed under parsimony, maximum likelihood, and Bayesian inference search algorithms.

Parsimony analysis: The phylogenetic analyses were conducted using PAUP* 4.0b10 (Swofford, 1999) under a heuristic search analyses with random addition sequence, 1000 replications with random input order, and one tree held at each step during stepwise addition. Bootstrap and jackknife values were calculated in TNT 1.1 (Goloboff *et al.*, 2008a), after 1000 iterations each. Bremer support values for the traditional search were calculated under tree bisection reconnection (TBR), and retained trees suboptimal by 30 steps. All characters were equally weighted and unordered.

Maximum likelihood: The maximum likelihood analysis was performed in IQ-Tree v. 1.5.6 (Nguyen *et al.*, 2015; Trifinopoulos *et al.*, 2016) using the Mk model of morphological character evolution Lewis, 2001 conditioned on sampling variable characters only (ascertainment bias correction; +ASC). The among-site rate variation was modeled using gamma distribution with eight discrete rate categories (+G8); the number of categories was selected from an empirically derived range of optimal values (Yang, 1994; Ronquist *et al.*, 2009; Harrison and Larsson, 2015). The node support was estimated using ultrafast bootstrap and SH-aLRT options with 1000 replicates each (Minh *et al.*, 2013).

Bayesian inference: We analyzed the data set using Bayesian inference as implemented in MrBayes v. 3.2.6 (Ronquist *et al.*, 2012). The data set was analyzed under the traditional Mk model (Lewis, 2001) with an ascertainment bias correction to account for scoring only variable morphological characters. Each analysis was performed with two independent runs of 5×10^7 generations each. We used the default settings of four chains (one cold and three heated) per each independent run. The relative burn-in fraction was set to 50% and the chains were sampled every 1000 generations. We set the temperature parameter to 0.01 as determined by preliminary runs to achieve chain mixing values in the optimal range (0.4 – 0.8). Convergence of independent runs was assessed through the average standard deviation of split frequencies (ASDSF $\ll 0.01$) and potential scale reduction factors [PSRF ≈ 1 for all parameters (Gelman and Rubin, 1992)]. We used Tracer v. 1.6 (Rambaut *et al.*, 2014) to determine whether the runs reached stationary phase and to ensure that the effective sample size (ESS) for each parameter was greater than 200. Results of the Bayesian runs were summarized as a majority-rule consensus tree of the post-burnin sample with a node support threshold of 75% (nodes with posterior probability support < 75% were collapsed).

4.6. Supplementary Text

4.6.1. Geographical and geological settings

The type series of †*Callichimaera perplexa* was collected in lower Upper Cretaceous marine rocks of the Churuvita Group, cropping out near Pesca, Department of Boyacá, Eastern Cordillera of Colombia (Supplementary Fig. S4.1), 150 km northeast of Bogotá, and 50 km southeast of Villa de Leyva (also spelled Villa de Leiva). The upper Cenomanian–lower Turonian Nocuatá Section is approximately 95 m thick, and includes the uppermost part of the Churuvita Formation at the base (Segments A and B) and the lowermost part of the San Rafael Formation at the top (Segment C) (Supplementary Fig. S4.2). Segment A (28 m) is composed at the base of 15.5 m of gray shales, and light-gray, micaceous, fossiliferous claystones. Three crustacean taxa, including *Callichimaera*, constitute the dominant macrofaunal elements, with occasional occurrence of scattered fish remains, ammonite aptychi, and small lingulid brachiopods. †*Callichimaera* is the largest arthropod element from this faunule, reaching a maximum carapace length of ~15 mm, while the associated shrimp reach ~10 mm in length, and the cumaceans ~5 mm in length (Supplementary Fig. S4.3). The uppermost portion of Section A (12.5 m) is covered/weathered. The overlying Segment B is composed of 11 m of silty sandstones, and thick beds of white–yellowish, slightly micaceous sandstones, representing the last occurrence of coarse–grained deposits along the section. Segment C lies above these thick layers of sandstone and is composed of ~56 m of gray fossiliferous shales with occasional indurated, gray, fossiliferous shale beds in the lower portion, interbedded at the top with fine–grained, silty sandstone lenses and non–calcareous nodules (Supplementary Fig. S4.2). Its lowermost portion (~25 m) is covered/weathered. The uppermost Segment C (~31 m) contains invertebrate assemblages typical of the lower–middle Turonian San Rafael and La Frontera formations in Colombia (Villamil and Arango, 1998; Feldmann *et al.*, 1999; Vega *et al.*, 2007b; Vernygora *et al.*, 2017) and of the Eagle Ford Group equivalent strata in Coahuila, Mexico (Vega *et al.*, 2007b; Guinot *et al.*, 2008). Abundant globulose foraminifera, teleosteii fish remains, ammonites such as *Hoplitoides* spp., *Collingnoniceras* sp., ?*Coilopoceras* sp., and ?*Romaniceras* sp. (Etayo–Serna, personal communication, 2011), abundant decapod crustaceans such as †*Cenomanocarcinus* Van Straelen, 1936 (Vega *et al.*, 2007b; Vega *et al.*, 2010; Luque, 2015a; Luque *et al.*, 2017b), and several shrimp and thalassinid remains, also occur within Section C.

The Churuvita Formation has been dated as Cenomanian, and the San Rafael Formation as lower to middle Turonian in age, using ammonites and foraminifera (Etayo-Serna, 1968a, 1979; Sánchez-Quiñonez and Tchegliakova, 2005; Vernygora *et al.*, 2017). Throughout the late Cenomanian–early Turonian, the rocks cropping out at the Nocuatá Section were deposited in the eastern margin of a NNE–SSW aligned epicontinental sea, limited to the west by a volcanic arc–trench–system (part of what is today the Central Cordillera), and to the east by the Guayana Craton (Mann *et al.*, 1994), covering most of what is today the emerged Colombian Andes Eastern Cordillera (Villamil, 1998; Villamil and Arango, 1998; Cáceres *et al.*, 2005) (Supplementary Fig. S1). A regional transgressive surface indicates the end of relatively shallow–water, coarse clastic sedimentation during the Cenomanian and the initiation of deeper–water, fine–grained sedimentation at the beginning of the Turonian (Etayo-Serna, 1968b; Villamil and Arango, 1998; Feldmann *et al.*, 1999).

The additional paratypes of †*Callichimaera perplexa* were collected in Lower Upper Cretaceous marine rocks of the Frontier Formation, Colorado Group, exposed just north of the Cumberland Gap, Southwestern Wyoming Province on the eastern edge of the Green River Basin, U.S.A., ~150 km northeast of Salt Lake City, Utah. The Frontier Formation is composed of five members; Chalk Creek, Coalville, Allen Hollow, Oyster Ridge and Dry Hollow members, and is comprised mostly of sandstones, shales and siltstones of both marine and non-marine origin. It is underlain by the Albian Aspen shale and overlain by the Coniacian-Santonian Hilliard Shale. The specimens were found in the light-grey shale of the middle portion of the Allen Hollow Member, in association with bivalves, lingulid–like brachiopods, undetermined algae, and scattered fish remains. Merewether *et al*. (1984) placed the base of the Allen Hollow Member at the beginning of the mid Turonian. Exact dating of the Allen Hollow Member has not been done; however, the underlying Coalville Member was dated to 91.1 Ma and the lower part of the overlying Hilliard Shale Formation at 88.9 Ma (Lanphere and Jones, 1978). Based on the stratigraphy of the area, the date of the Allen Hollow Member would be closer to 91.1 Ma considering there are two other interferring members.

4.6.2. Supplementary taxonomic remarks

The superfamilies Homolodromioidea Alcock, 1900a, Koniodromitoidea Karasawa, Schweitzer, and Feldmann, 2011, and Glaessneropsoidea Patrulius, 1959, differ from Callichimaeroidea in the possession of subchelate P4 and P5, eyes protected by well-defined orbits and an augenrest (except in Glaessneropsoidea), a subhepatic region that is usually inflated, the postcervical groove usually present, the pleon bearing uropods or uropodal plates, and pleon in males close to the coxae (Alcock, 1900a; Števčić, 2005; Schweitzer and Feldmann, 2009; Karasawa *et al.*, 2011). Similarly, the superfamily Dromioidea De Haan, 1833, is distinguished by its well-developed orbits, the inflated subhepatic regions, usually developed postcervical groove, a narrow sternum bearing sternal projections, the presence of a sterno-coxal depression, pleonite 6 usually bearing triangular epimeres, the possession of uropodal plates, and last pair of pereiopods usually prehensile, carried subdorsally (Ortmann, 1892a; Wright and Collins, 1972; McLay, 1993, 1999; Guinot and Tavares, 2003; Guinot, 2008; Schweitzer and Feldmann, 2010a; Karasawa *et al.*, 2011). Furthermore, the possession of small mxp3 coxae that never touch, sternites 1-3 distinct ventrally, and the absence of a postcervical groove (except for Diaulacidae Wright and Collins, 1972, and Xandarocarcinidae Karasawa *et al.*, 2011), ensures a separate phylogenetic affiliation from the most primitive brachyurans. †Callichimaeridae can also be differentiated from Homoloida by the lack of an evident 'linea' (often referred to as 'linea homolica'), the characteristic 'homolid press-button' (absent in Mithracitidae Števčić, 2005), a telson projecting between the coxae of maxillipeds, the absence of an augenrest (except in Latreillidae Stimpson, 1858), and the lack of sterno-coxal and sterno-pleonal depressions (Guinot, 1991; Števčić, 2005; Scholtz and McLay, 2009; Karasawa *et al.*, 2011).

Third maxillipeds equipped with serrated or spinose ischium (*crista dentata*) are known from adult and juvenile forms among many brachyuran and non-brachyuran decapods, including, but not exclusive to, some astacideans (e.g., Harlioglu, 2003, 2008), achelates (e.g., Suthers and Anderson, 1981; Guerao *et al.*, 2006), anomurans (e.g.,Martin and Felgenhauer, 1986; Ahyong and Baba, 2004; Hoyoux *et al.*, 2009; McLaughlin and Lemaitre, 2009), and early-diverging brachyurans (e.g., McLay, 2001; Guinot and Tavares, 2003; McLay and Ng, 2007). Nonetheless, whether the spiniform structures found in some eubrachyurans (e.g., Williams, 1978; Skilleter and Anderson, 1986; Marquez *et al.*, 2003; Scholtz and McLay, 2009) is homologous with the '*crista dentata*' sensu stricto is unclear (Ng *et al.*, 2008). Scholtz and

McLay (2009: p. 425) stated that: “the *crista dentata* (…) is a plesiomorphic reptant character that is present in the homolodromioids, dromiids, dynomenids, and homolids (except latreilliids)”, but lost once in the most recent common ancestor of the clade that unites Raninoida, Cyclodorippoida, and Eubrachyura. The *crista dentata* present in †*Callichimaera* possesses four to five acute spines, positioned in the inner border of the mxp3 ischium (Supplementary Fig. S4.4e). *Crista dentata* and mxp3 bearing a long palp are the plesiomorphic conditions for Decapoda, but absent in higher podotremes and Eubrachyura.

4.6.3. Supplementary systematic remarks

Precise phylogenetic placement of †*Callichimaera* within Brachyura is problematic because of a) its ‘chimaeric’ nature and b) possession of multiple distinctive characters typical of several fossil and extant early-branching and ‘higher’ Brachyura clades (main text, Fig. 4.2), but not collectively seen in any one taxon. These characters of †*Callichimaera* include:

i) A carapace outline with broad branchial regions and a dorsal pattern of longitudinal keels and grooves that is more reminiscent of some lobsters and palaeocorystid crabs, respectively (light grey, Fig. 4.2a), than it is of most anomurans or brachyurans.
ii) A third maxilliped that bears a *crista dentata* (red, Fig. 4.2b), the ancestral condition for larval decapods and adult lobsters, most anomurans, early-branching brachyurans like Homolodromioidea, and most Homoloidea. The alternate character state of an operculiform third maxilliped shielding the buccal frame is present in two clades: the ‘higher’ Dromioidea, and higher podotreme brachyurans plus eubrachyurans.
iii) Spanner-like chelipeds similar to those seen burrowing groups like Hippoidea (Anomura), Raninoidea (Brachyura), and the callichimaeroid-like †*Retrorsichela* (yellow, Fig. 4.2a–b).
iv) The shape, size, position, and function of paddle–like limbs, e.g., *Callichimaera*’s flattened pereiopods 2–3 (P2–P3), which are highly variable among anomurans and brachyurans. In hippoids and raninoids, the pereiopods are specialized digging tools, while in brachyurans such as Portunoidea, Orithyioidea, some Calappoidea (i.e., Matutidae), and some extinct †Necrocarcinoidea (i.e., †*Cenomanocarcinus*), they likely facilitate both swimming and digging (green, Fig. 4.2a–b). †*Callichimaera* possesses reduced P4–P5 (blue, Fig. 4.2a–b),

which occur in some anomurans (e.g., Paguroidea, or hermit crabs), some podotreme brachyurans (e.g., Homolodromioidea, Cyclodorippoidea), and early-branching eubrachyurans (e.g., Dorippoidea), but mostly with claw-like modifications to grab or grasp, absent in the new taxon.

v) A symmetrical pleon, unlike that of hermit crabs but as as in most Brachyura, it lacks articulating rings between pleonites (purple, Fig. 4.2a–b). The presence of uropods or uropodal plates at the posterior end of the pleon is plesiomorphic for Decapoda (shrimps, lobsters, anomurans and early-branching brachyuran clades have them), but these are absent in *Callichimaera*, and the most inclusive podotreme clades plus Eubrachyura.

vi) A puzzling sternal configuration due to the dissimilarity in shape and size of its sternites. The large S5–S6 vaguely resemble those of *Retrorsichela* (doubtfully Anomura: Galatheoidea) and *Heikeopsis* (Eubrachyura: Dorippoidea) (orange, Fig. 4.2b), but still its sternal configuration is unmatched among brachyurans (Guinot *et al.*, 2013).

vii) Pediform mouthparts with *crista dentata*, the marked difference between legs P2–P3 and legs P4–P5, the unusual pattern of sternal sutures, the shape and size of the sternites, and the orbital and optical configuration, are all inconsistent with diagnostic characters for the more inclusive podotreme clades (e.g., Raninoida and Cyclodorippoida) and eubrachyurans (Supporting Fig. S4.10).

viii) Finally, large eyes lacking true orbits and orbital fissures that also occur in some ancient brachyurans such as *Ekalakia* (Dromiacea: Glaessneropsidae), and several homoloids (dark grey, Fig. 4.2a–b see also Chapter 6).

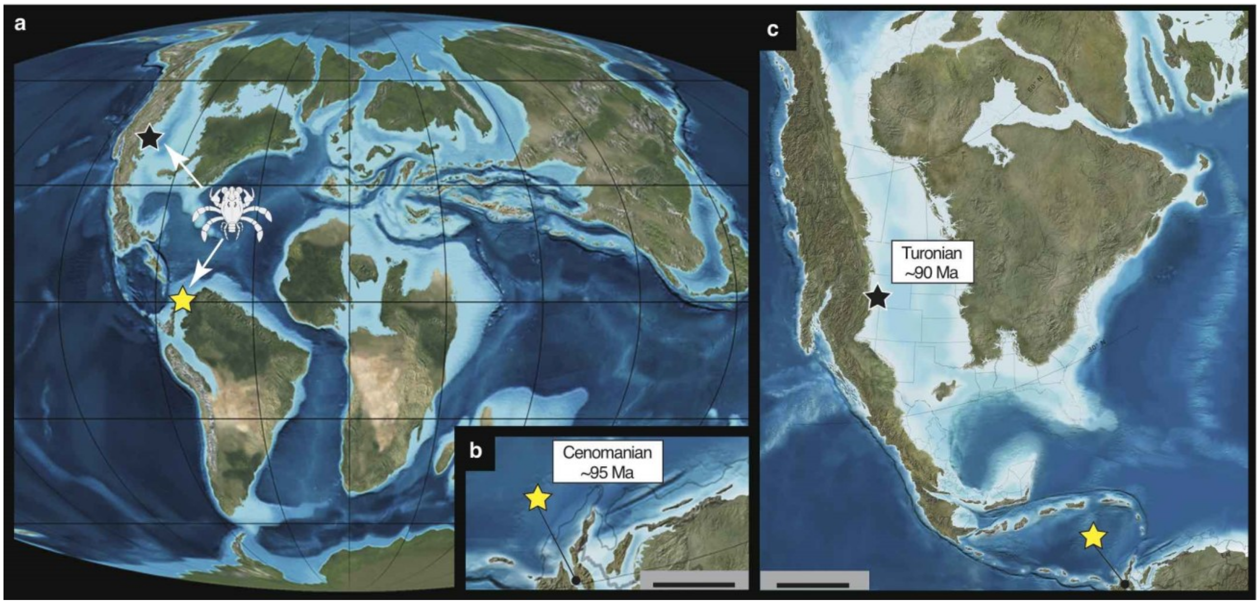
The chimaeric nature of †*Callichimaera* is due to a combination of primitive and derived traits that place it in an intermediate position between the oldest groups of true crabs (i.e. Dromiacea and Homoloida), and all of the more derived podotreme and sternitreme clades (Fig. 4.3, Supplementary Figs S4.9–S4.10). †*Callichimaera* fills a major gap in crab evolution, and bring extra support to the hypothesis that podotreme brachyurans do not represent a monophyletic assemblage but a rather a diverse evolutionary grade increasing in complexity. The phylogenetic proximity of several of the more inclusive podotreme clades to the highly derived Eubrachyura led us to recognize an unnamed and unranked monophyletic clade comprised by the most inclusive lineages of extant brachyurans and their fossil relatives — i.e., Raninoida

(Cyclodorippoida + (Eubrachyura)), and a stem-group formed by extinct lineages, e.g., Etyoida, Torynommoida, Dakoticancroida (Supplementary Figs S4.8–S4.10), sharing apomorphies not seen, in whole or in part, among less inclusive crab clades. The adult morphological characters that support this clade include a) the presence of truly operculiform maxillipeds 3, b) the palp of maxillipeds 3 articulating in the same plane as the rest of the operculum, c) the lack of true crista dentata on the inner margin of the ischium in maxillipeds 3 (homoplasious in latreiilids), d) the presence of well-defined orbits (homoplasious in dromioids), and e) the presence of hexagonal shaped facets in adults, suggestive of apposition eyes (and apposition-derived parabolic superposition eyes in some taxa). These apomorphic traits strongly differ from the plesiomorphic conditions seen among the less inclusive brachyuran clades Homolodromioidea, most Dromioidea, Homoloidea, and Callichimaeroidea n. superfam. However, we cannot say whether the retention of larval apposition eyes into adulthood was already present in the most recent common ancestor for Callichimaeroidea and the most inclusive podotremes + Eubrachyura, or whether it happened independently in all of these groups.

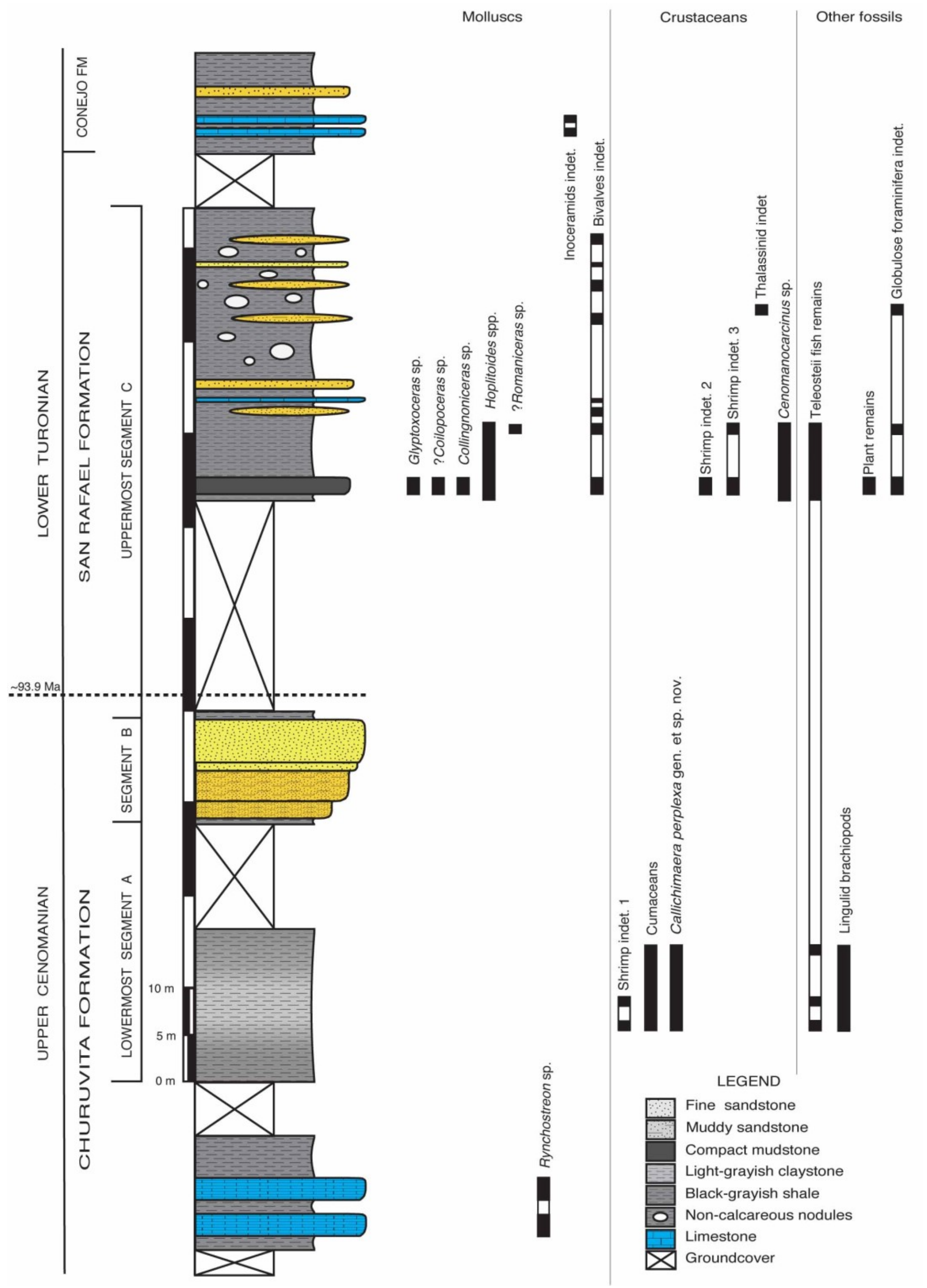
4.6.4. Additional remarks

Although †*Callichimaera* strongly resembles the late larval (megalopa) stage of some crabs, both the overall body size and several key anatomical features of larger individuals indicate that they were mature adults. The megalopa larvae of brachyuran crabs tend to measure ~1-2 mm carapace width on average Hines, 1986. The size of megalopae varies little within a species; even the very large megalopae of the Dungeness crab, which have been reported to vary significantly in size, nonetheless vary only slightly (2.2-4.5 mm CW) (DeBrosse *et al.*, 1990). While megalopae size is positively related adult size (Hines, 1986), and there are some examples of exceptionally large megalopa, even the megalopae of the giant Japanese spider crab *Macrocheira kaempferi* (adult leg span up to ~4 m) — the largest living arthropod — measures only ~ 2 mm carapace width (Tanase, 1967). Further, when megalopa size is corrected for adult size there is no significant difference in size among brachyuran families (Hines, 1986). Among anomurans, the megalopa of the large robber or coconut crab *Birgus latro* (adult leg span up to ~1 m), reaches ~4 mm (Reese and Kinzie, 1968), as also do the megalopae of pagurids like *Dardanus* and some parapaguroid hermit crabs (Harvey *et al.*, 2014). †*Callichimaera* specimens are two to eight times larger than the largest known living and fossil megalopa larvae, and comprise a larger range of sizes than typical crab megalopae do. Also, crab larvae swim by either beating the maxillipeds 1–2 (zoeae stages) — usually aided by the pleon— or by biramous pleopods on the pleonites 2–5 (megalopa) (Harvey *et al.*, 2014; Martin, 2014). Instead, †*Callichimaera* swam presumably by motion of its strongly flattened pereiopods P2–P3, which are unknown in fossil or extant crab megalopae. Furthermore, sexual dimorphism in crabs does not become evident until several molts beyond metamorphosis into the first juvenile crab stage, usually around crab stage 6 or 7 (Flores and Negreiros-Fransozo, 1999; Negreiros-Fransozo *et al.*, 2007; Guerao and Rotllant, 2009; Arruda and Abrunhosa, 2011; Negreiros-Fransozo *et al.*, 2011; Guerao *et al.*, 2012). Crab megalopae of most anomurans, dromiaceans, homoloidans, raninoidans, and several eubrachyurans (calappids, corystids, etc.) lack the primary and secondary sexual traits seen in early to adult crab stages (Martin *et al.*, 2014), and have either fully developed uropods or relicts of uropodal plates. The †*Callichimaera* specimens found to date do not possess uropods or uropodal remains, and several of the most well-preserved specimens show sexually dimorphic characteristics such as sclerotonized gonopods and dimorphic pleonites; sexual traits never seen in megalopa larval stages.

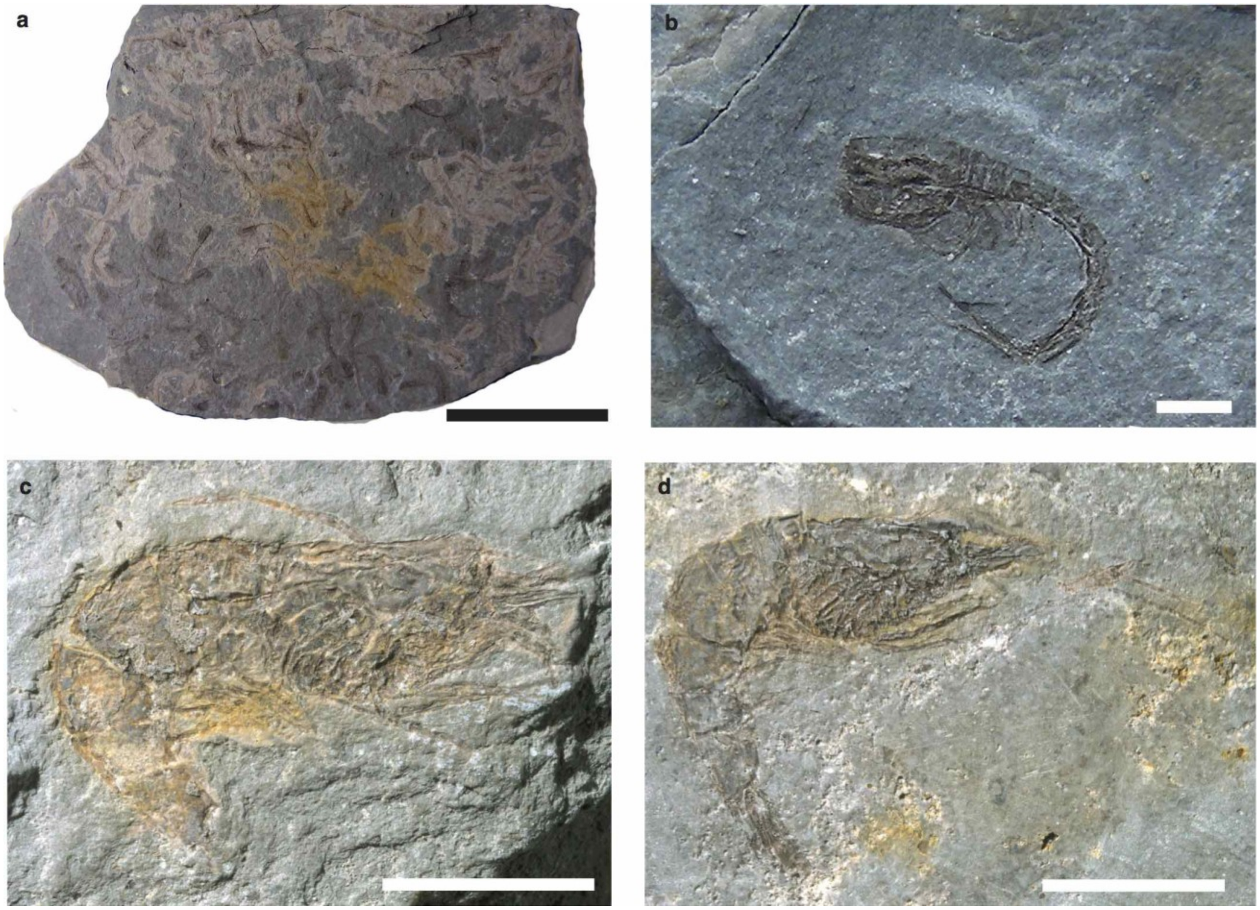
†Callichimaeridae fam. nov., from the upper Cenomanian of Colombia, adds to the growing evidence that the tropics may have acted as a cradle of crab diversification since at least the Early Cretaceous (Luque *et al.*, 2013). Recent discoveries from northern South America represent either the oldest, or one of the oldest fossil records for several ancient crab families and superfamilies, including the oldest †Orithopsidae (Luque *et al.*, 2012; Karasawa *et al.*, 2014; Luque, 2014b; Schweitzer *et al.*, 2016) (superfam. †Necrocarcinoidea), †Palaeocorystidae (Luque *et al.*, 2012) (superfam. Palaeocorystoidea), †Diaulacidae (Gomez *et al.*, 2015, Luque, in press) (superfam. Dromioidea), and the oldest members of the section Eubrachyura, or 'higher' true crabs (superfam. Dorippoidea) (Luque, 2015b). Also, other findings include some of the oldest †Cenomanocarcinidae Vega *et al.*, 2010 (superfam. Necrocarcinoidea), and †Mithracitidae van Bakel *et al.*, 2012b (superfam. Homoloidea) (Fig. 3, yellow stars). Together, these occurrences suggest that many brachyuran crab clades previously considered to have originated at higher latitudes had their origins in tropical to subtropical regions.



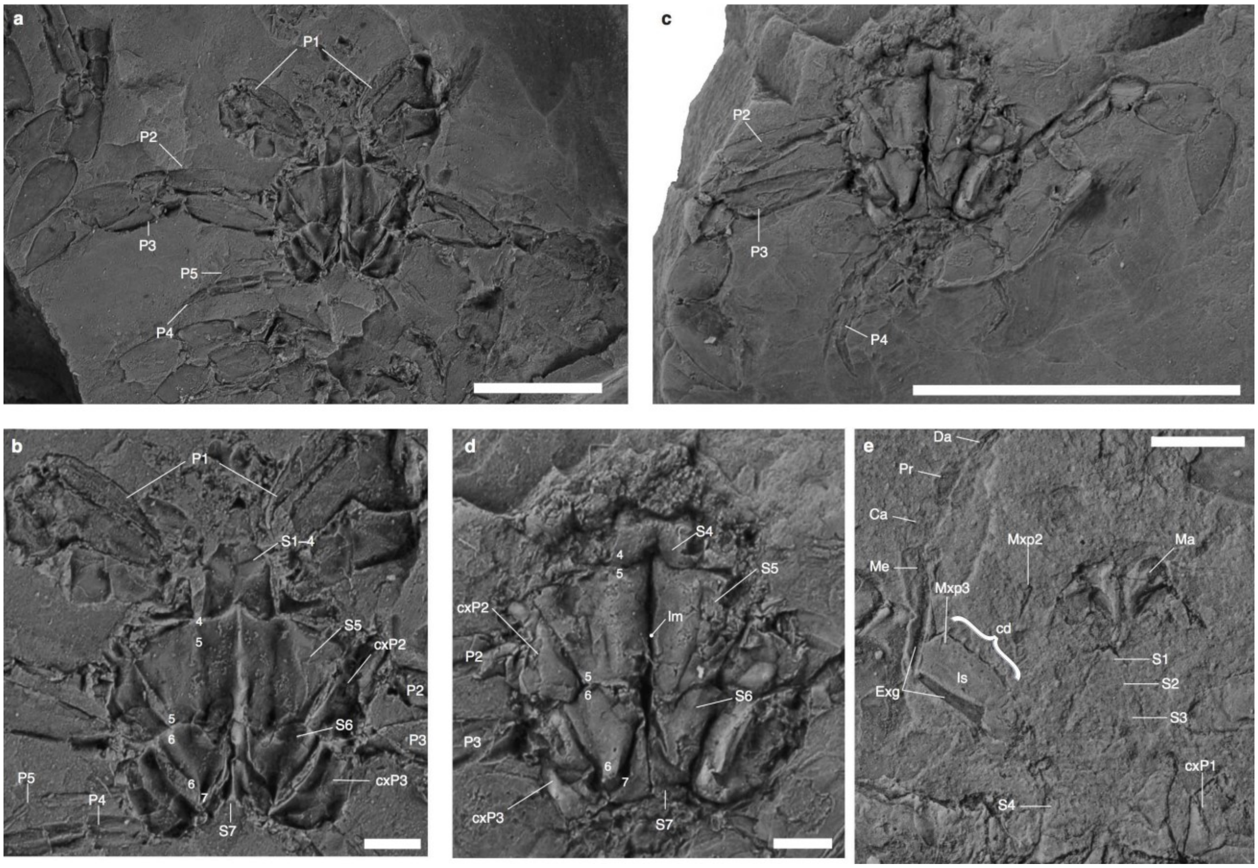
Supplementary Figure S4.1. Paleogeographic map during Early Late Cretaceous times (~95–90 Ma). (a) localities where the holotypes and paratypes (Colombia, yellow star; USA, black star) of †*Callichimaera perplexa* gen. et sp. nov. were discovered. (b) Close-up showing the tropical South American type locality of †*Callichimaera*, Upper Churuvita Formation (~95 Ma), Boyacá, Colombia. (c) Close-up showing the North American locality, Frontier Formation (~90 Ma), Wyoming, USA. (Base maps modified from http://cpgeosystems.com, data retrieved August 20, 2015. Paleomaps copyright: Ron Blakey). Scale bars: b, 500 km; c, 1000 km.



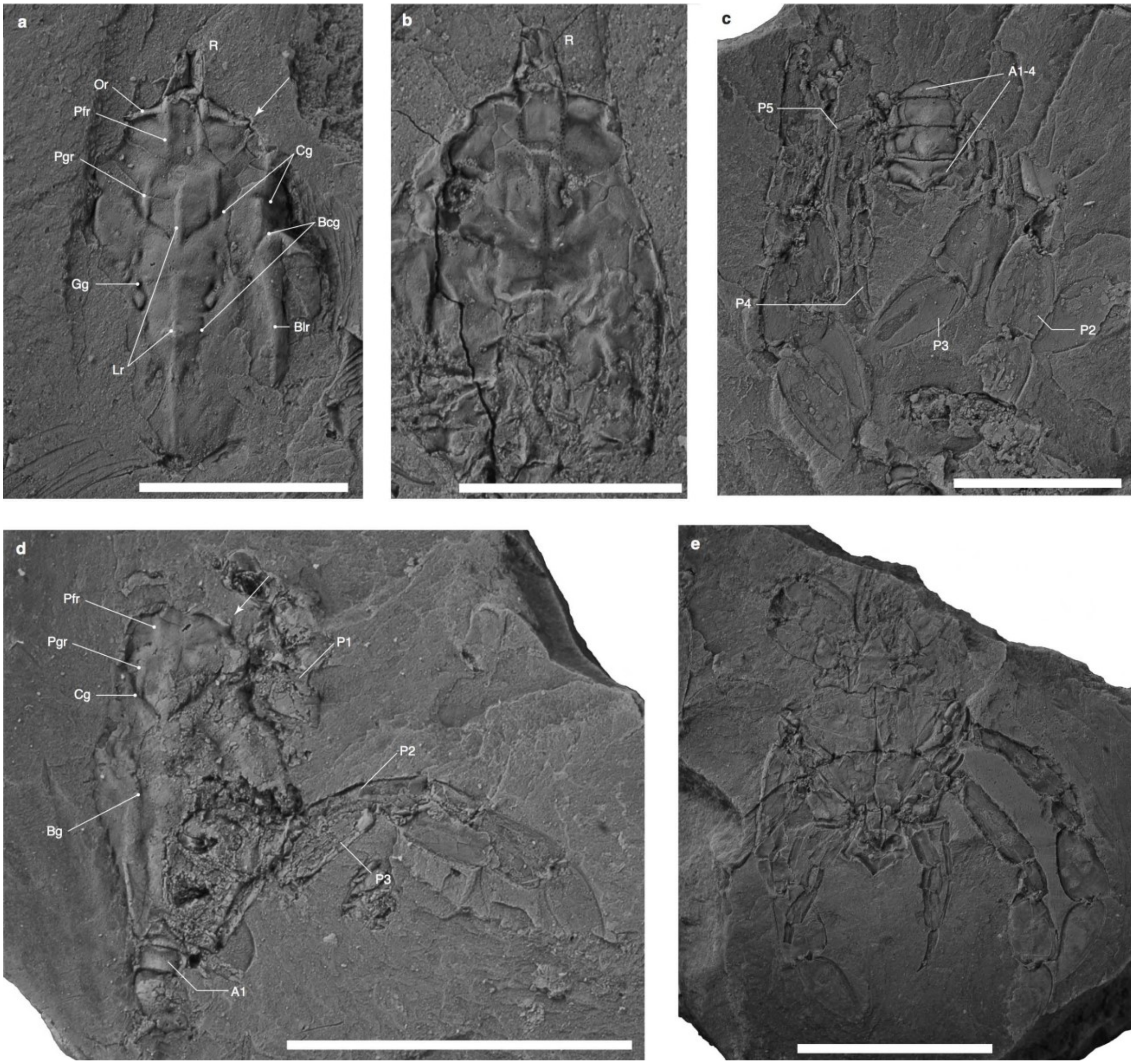
Supplementary Figure S4.2. Stratigraphic column of the Cenomanian–Turonian Churuvita Group outcropping at the Nocuatá Section, Department of Boyacá, Colombian Eastern Cordillera. For each taxon, black and white columns indicate where macrofossils were recovered or not along the section, respectively. Dashed line indicates the tentative Cenomanian–Turonian boundary (~93.9 Ma).



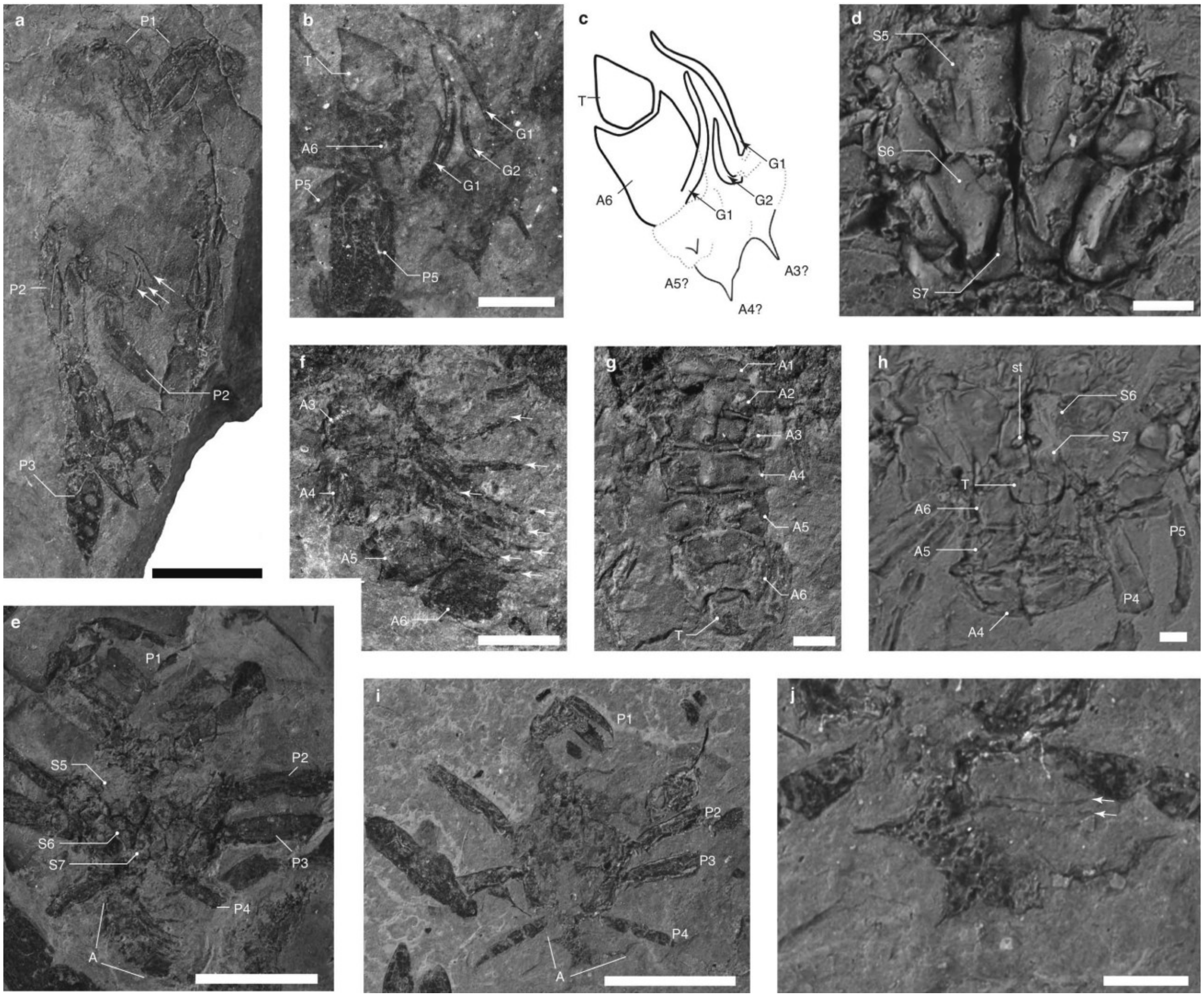
Supplementary Figure S4.3. Crustacean–dominated faunule at the Nocuatá Section. (a) Cumacean–rich surface showing the high density and random orientation of cumaceans specimens associated with †*Callichimaera perplexa* gen. et sp. nov. (b) Sample, cumacean specimen showing details of the carapace, thoracopods, and pleon. (c–d) unidentified shrimps. Scale bars: a, 10 mm; b, 1 mm; c–d, 5 mm.



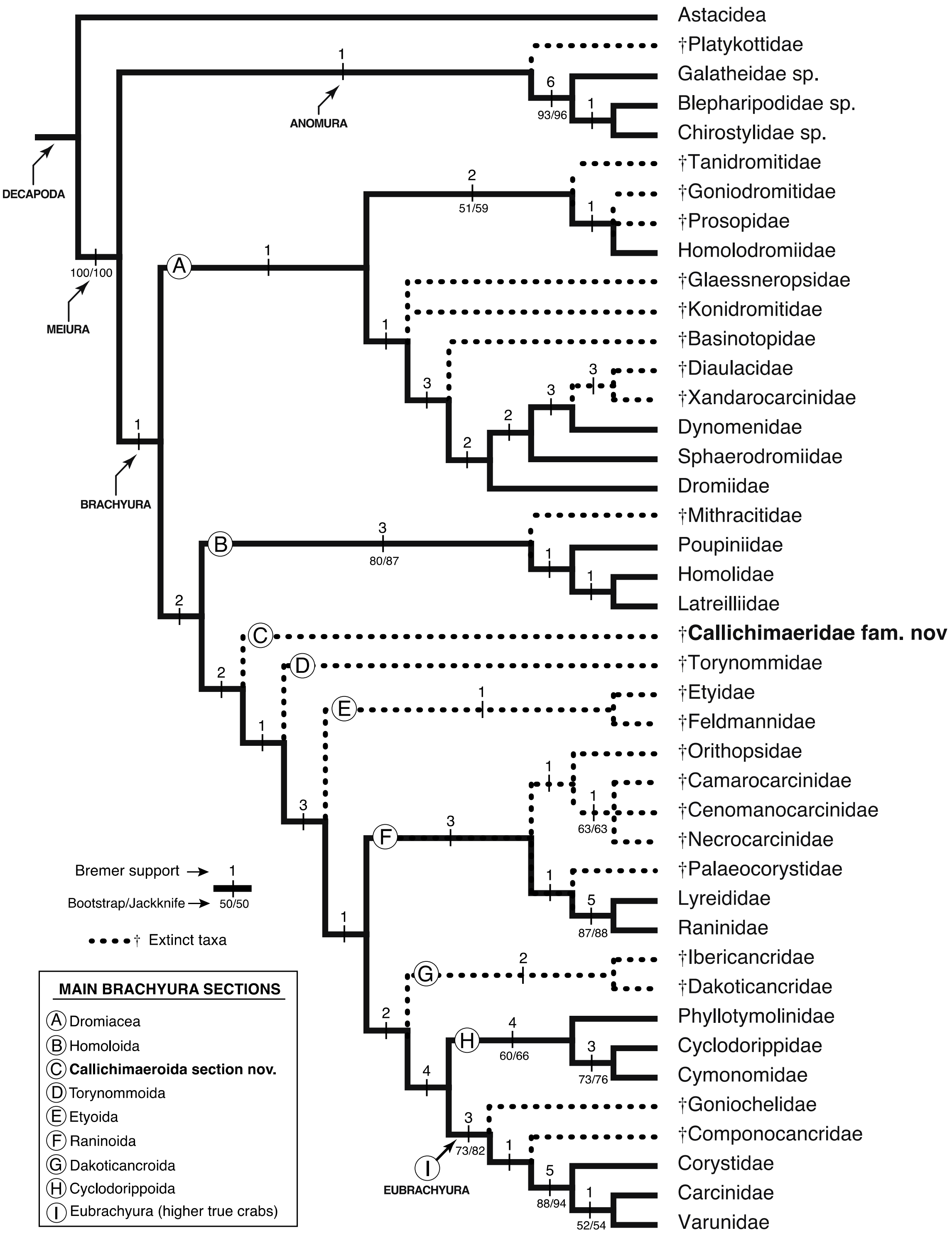
Supplementary Figure S4.4. Vetral and appendicular features of †*Callichimaera perplexa* n. gen. n. sp. Specimens coated with ammonium chloride. (a–b) Paratype IGM p881196, ventral view: (c) thoracic sternum, chelipeds P1, and legs P2–P5; (d) close–up of thoracic sternum showing the coxae of P2–P3, the sternites, and the sternal sutures. (c–d) Paratype IGM p881216, ventral view: (c) thoracic sternum and legs P2–P4; (d) close–up of thoracic sternum showing the coxae of P2–P3, the sternites, and the sternal sutures. (e) Holotype IGM p881215, ventral view, close–up showing details of the sternal crown (sternites 1–4) and the mouthparts. Abbreviations: Ca: carpus; cd: crista dentata; cxP1: coxa of cheliped or claw; cxP2–cxP3: coxae of legs P2–P3; Da: dactylus; Exg: exognath of third maxilliped; Is: ischium; lm: linea media; Ma: mandibulae; Me: merus; Mxp2–Mxp3: maxillipeds 2 to 3; P1: cheliped or claw; P2–P5: pereiopods or walking legs 2 to 5; S1–S7: sternites 1 to 7; 4/5 to 6/7: sternal sutures between sternites 4–5 to 6–7. Scale bars: a, 5 mm; b, d–e, 1 mm; c, 10 mm.



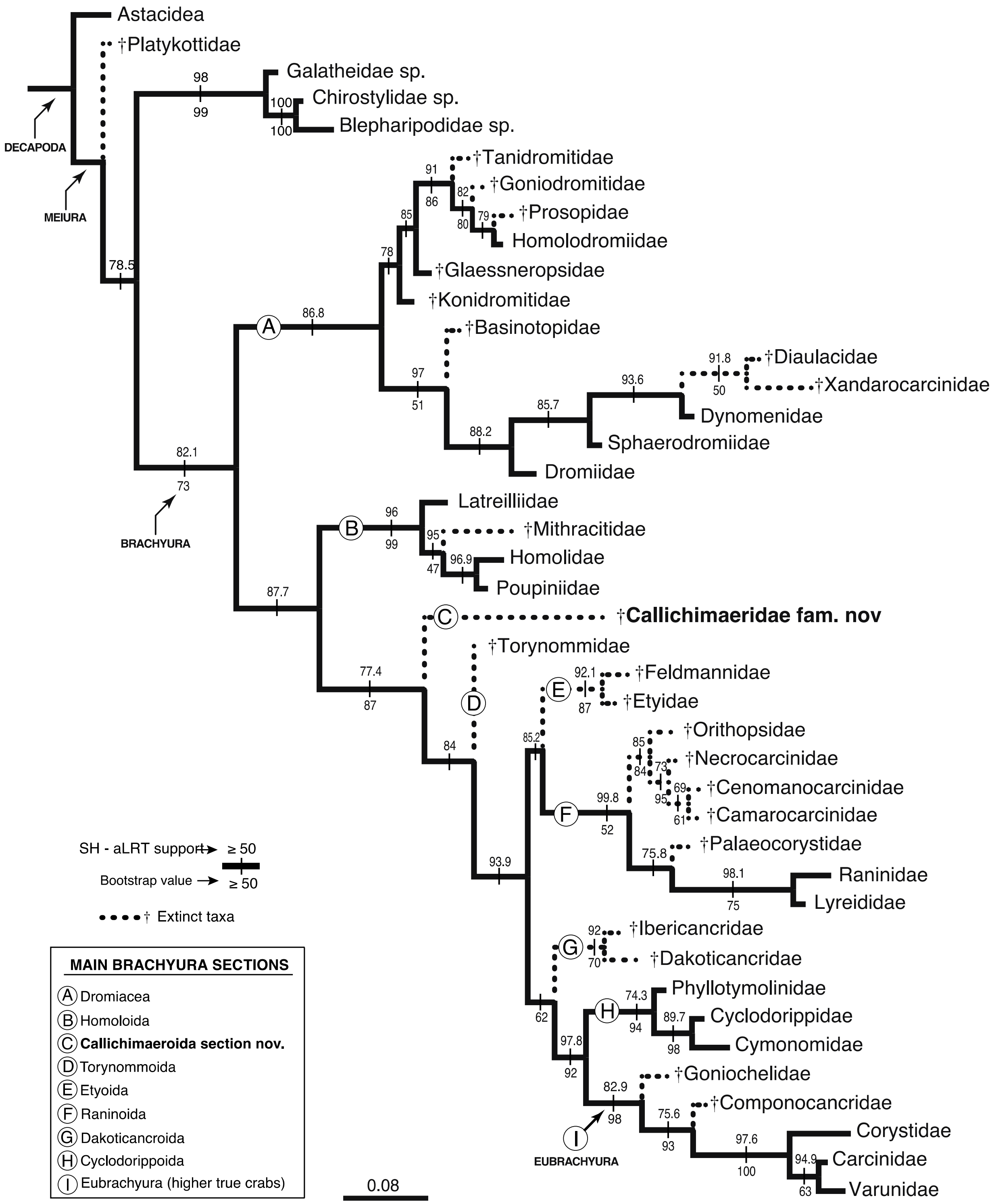
Supplementary Figure S4.5. Dorsal and appendicular features of †*Callichimaera perplexa* n. gen. n. sp. Specimens coated with ammonium chloride. (a) Paratype IMG p881203, details of dorsal view highlighting the distinct cervical, branchial, and gastric grooves, and the longitudinal, branchial, the orbital, postfrontal, and protogastric ridges. White arrow points to the position of an anterior protrusion. (b) Paratype IGM p881204, dorsal counterpart showing the fine granulation at the median portion of the carapace. (c) Paratype IMG p881217, dorsal view showing the legs P2–P5 and the pleonites bearing an axial tubercle. (d) Paratype IMG p881218, moderately preserved dorsal view showing legs P1–P3, a narrow pleon, cervical and branchial grooves, and postfrontal ridges. (e) Paratype IGM p881214, ventral view showing the sternites, legs P2–P5, and pleon. Abbreviations: A1–4: pleonites 1 to 4; Bcg, branchio–cardiac groove; Blr, branchial longitudinal ridge; Cg, cervical groove; Lr, axial longitudinal ridge; Gg: metagastric / urogastric groove; Or, orbital ridge; P1: cheliped or claw; P2–P5: pereiopods or walking legs 2 to 5; Pfr, post–frontal ridge; Pgr: protogastric ridge. Scale bars: a–c, 5 mm; d–e, 10 mm.



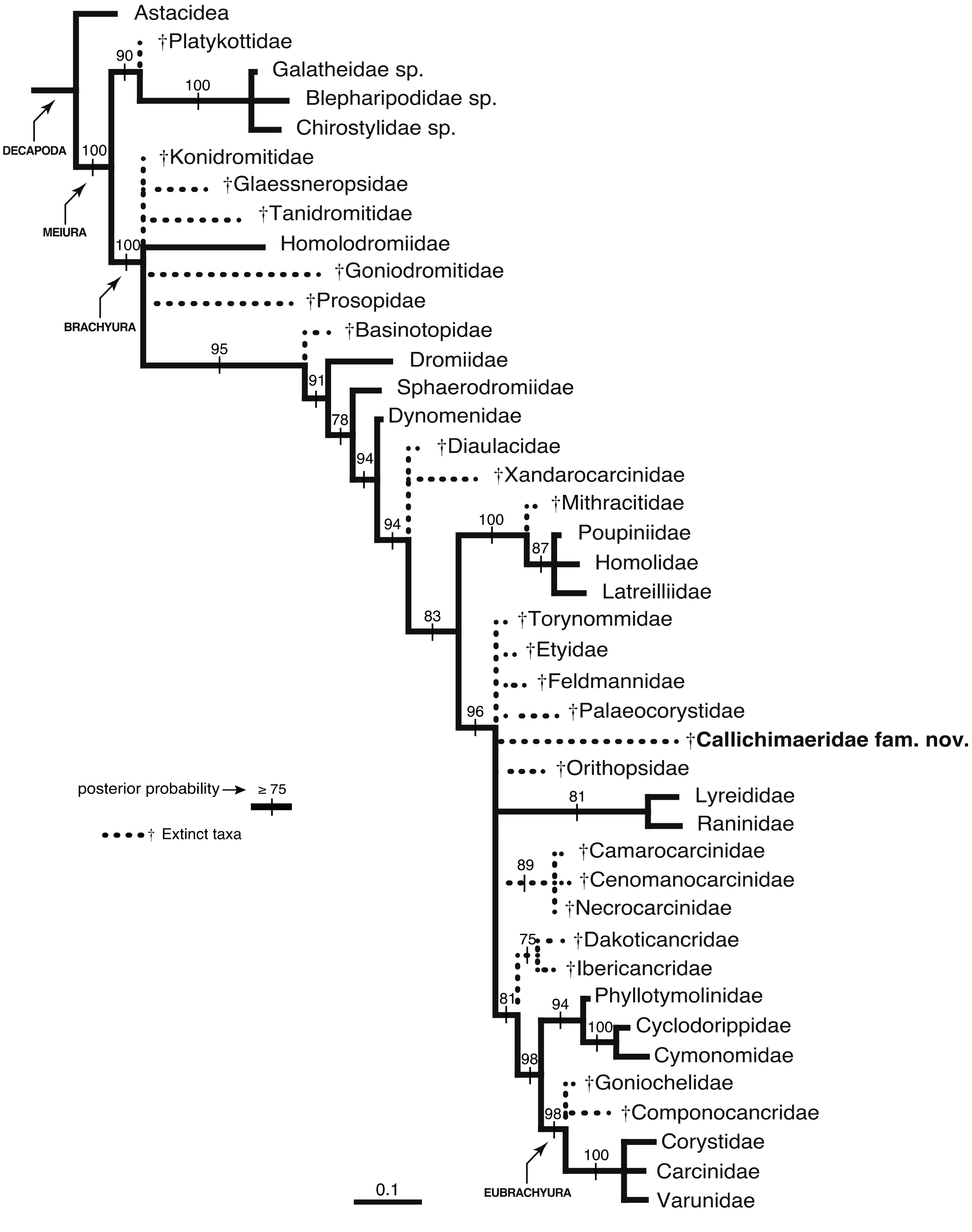
Supplementary Figure S4.6. Pleonal and uropodal features of †*Callichimaera perplexa* n. gen. n. sp. Specimens coated with ammonium chloride. (a–c) Paratype IGM p881202, male, ventral view: (a) specimen showing the chelipeds, pereiopods, and pleon. Arrows indicate the sclerotized gonopods 1–2; (b) close–up showing the male's last pleonites, telson, and sclerotized gonopods 1–2. (c) Line drawing of B. (d) Paratype IGM p881216, male, ventral view, close–up of thoracic sternum showing sternites 5–7; sternites 7 lacking spermatheca. (e–f) Paratype IGM p881209b, female, ventral view: (e) specimen showing the unfolded pleon, cheliped, and pereiopods; (f) close–up of female pleon, showing multiple pairs of pleopods (arrows). (g) Paratype MUN-STRI 27045-06, female, dorsal view showing the pleonites and telson. (h) Paratype IGM p881206, female, ventral view, showing pleonites, telson, sternites 5–7, and sternites 7 bearing a paired spermatheca. (i–j) Paratype IGM p881217, male, ventral view: (i) specimen of small size preserving the cheliped, pereiopods 2–4, and pleon; (j) close–up of I, showing the first pleonites in side view, bearing an acute protuberance axially, and slender gonopods (arrows). Abbreviations: A: pleon; A1–A6: pleonites 1 to 6; G1–G2: male gonopods 1 and 2; P1: cheliped (claw); P2–P5: pereiopods (legs) 2 to 5; S5–S7: sternites 5 to 7; st: spermatheca; T: telson. Scale bars: a,i, 5 mm; b, d, f–h, j, 1 mm; e, 10 mm.



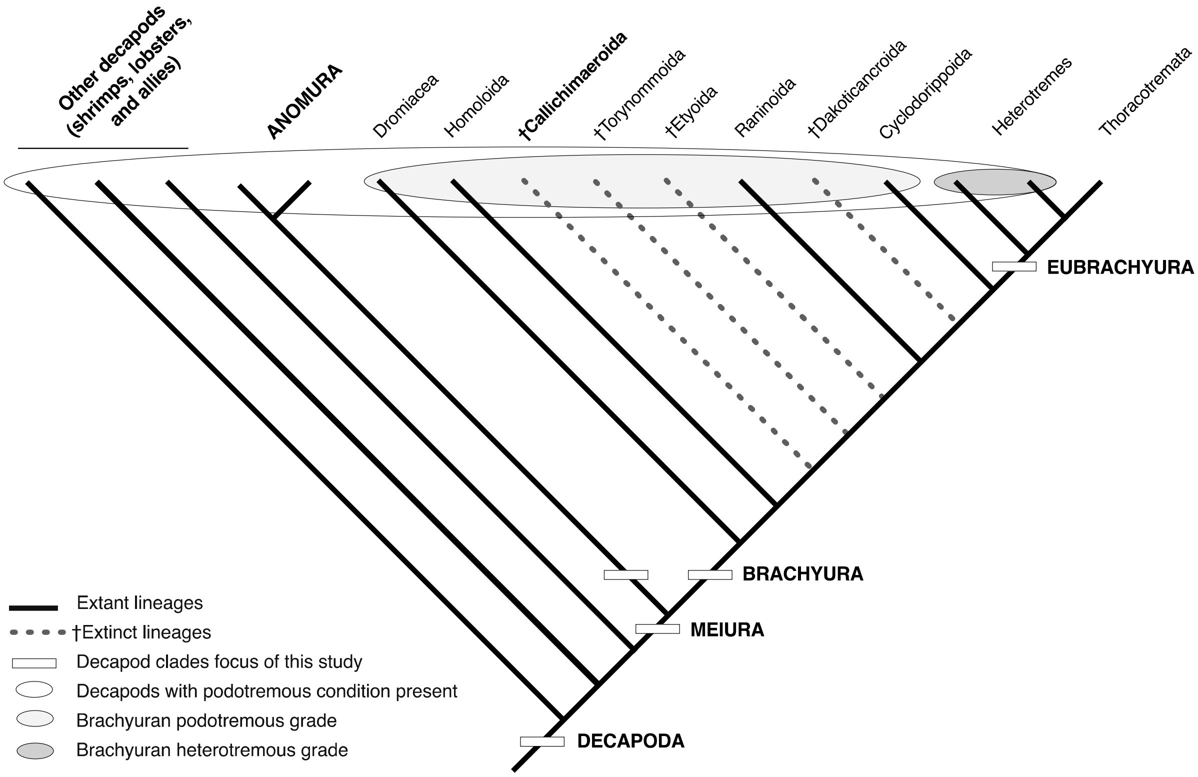
Supplementary Figure S4.7. Strict consensus tree of nine most parsimonious trees for the nine major brachyuran sections and podotremous brachyuran families, including †Callichimaeridae n. fam. Each capital letter in circle represents one of the nine main sections (as identified in the legend). Tree length (TL)= 256 steps; consistency index (CI)= 0.523; retention index (RI)= 0.793; rescaled CI (RC)= 0.415. Major brachyuran lineages indicated by capital letters A to I. Bremer support indicated above branches; Bootstrap (left) and Jackknife (right) values indicated below branches. Terminal taxa indicated by a dagger (†) are extinct.



Supplementary Figure S4.8. Maximum likelihood topology with the nine major brachyuran sections and podotremous brachyuran families, including †Callichimaeridae n. fam. Each capital letter in circle represents one of the nine main sections. Major brachyuran lineages indicated by capital letters A to I. SH-aLRT support values indicated above branches; bootstrap support values indicated below branches. Terminal taxa indicated by a dagger (†) are extinct.



Supplementary Figure S4.9. Bayesian majority-rule consensus topology of the post-burnin sample of trees for fossil and extant podotremous brachyuran families, including †Callichimaeridae n. fam. Posterior probability support values indicated above branches. Branches with posterior probability support < 75% are collapsed. Terminal taxa indicated by a dagger (†) are extinct.



Supplementary Figure S4.10. Cladogram of the main fossil and extant lineages constituting the monophyletic Brachyura. White oval indicates presence of the podotreme condition in males. Light grey oval indicates the brachyuran podotremous grade; dark grey oval indicates the eubrachyuran heterotremous grade. Terminal taxa indicated by a dotted line and a dagger (†) only known from fossil representatives.

Chapter 5. Checklist of fossil decapod crustaceans from Tropical America, Part I: Anomura and Brachyura

5.1. Introduction

New paleontological discoveries made mostly during the last two decades have dramatically expanded our understanding of the crustacean fossil record from the New World's tropics. Recent works on fossil and extant anomurans and brachyurans (Hendrickx, 1995; Magalhães, 2003; Ng *et al.*, 2008; De Grave *et al.*, 2009; Boyko and McLaughlin, 2010; McLaughlin *et al.*, 2010; Osawa and McLaughlin, 2010; Schweitzer *et al.*, 2010; Bracken-Grissom *et al.*, 2013; Jagt *et al.*, 2015; among many others) have been pivotal to the synthesis of the current state-of-knowledge of marine, terrestrial, and freshwater fossil decapods in tropical America; one of the most diverse regions on Earth. These new discoveries, together with novel phylogenetic hypotheses, and re-examinations of several previous findings, call for an urgent revision of the crustacean fossil record from tropical America, and are the motivation behind the present checklist. In this work, we focus on the fossil decapods from the tropical Western Hemisphere and the need to put them into updated temporal, geographic, and systematic contexts.

The tropics are defined as the regions surrounding the Equator, extending roughly from the Tropic of Cancer (~23.3˚ N) to the Tropic of Capricorn (~23.3˚ S). In addition to the tropical occurrences of fossil anomurans and brachyurans, we have included records from subtropical areas ranging in latitude from ~30˚ N to ~30˚ S (Fig. 5.1). Since the neotropical region engulfs most of South America, here we restrict the South American fossil records to those north of 30˚ S latitude. The Caribbean, for the purpose of our work, is considered to be the non-continental land surrounded by the Caribbean Sea, and mostly positioned on the Caribbean tectonic plate. The fossil occurrences have been grouped into three main geographic regions: 1) northern South America, with records from Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, and Venezuela; 2) Central America and southern North America, with records from Belize, Costa Rica, Honduras, southern Florida, Mexico, and Panama; and 3) the Caribbean Islands and nearby areas, with records from Anguilla, Antigua, Aruba, Bahamas, Barbados, Bermuda, Bonaire, Cuba, Curaçao, Dominican Republic, the Grenadines, Haiti, Jamaica, Puerto Rico, Saint Bartélemy, Saint Martin, and Trinidad (Fig. 5.1). To the best of our knowledge, these are the tropical American countries, states, territories, or islands from where fossil anomurans and brachyurans have been either reported in the literature, or found as unpublished material in museum collections (e.g., USNM, MNHN) and reported here. Other tropical American countries, territories, or islands not listed or mentioned lack known brachyuran or anomuran fossils.

This work provides not only an updated and detailed list of fossil anomurans and brachyurans from tropical America, but also includes several new records and a re-examination of the systematic placement of problematic taxa. Although some genera such as ††*Lobonotus* A. Milne-Edwards, 1863, ††*Araripecarcinus* Martins-Neto, 1987, ††*Tepexicarcinus* Feldmann, Vega, Applegate and Bishop, 1998b, ††*Prehepatus* Rathbun, 1935b, and ††*Roemerus* Bishop, 1983b, still have unclear systematic affinities due to convergence, incompleteness of their carapaces, and/or poor preservation (e.g., Bishop, 1985; Vega *et al.*, 1995b; Vega *et al.*, 2005; Schweitzer *et al.*, 2006b; Vega *et al.*, 2006a; Jagt *et al.*, 2010; Jagt *et al.*, 2014; Ossó *et al.*, 2014; Luque, 2015a, 2015b), the systematic position of most other families, genera, and species here included have been verified by us and are, to the best of our knowledge, as accurate and updated as we can currently confirm. As a result, we recognize the occurrence in the tropical Americas of three superfamilies, six families, eight genera, and more than 10 spp. of anomurans ('false' crabs, hermit crabs, squat lobsters, and allies), and at least 26 superfamilies, more than 61 families, 153 genera, and over 282 spp. of brachyurans ('true' crabs). New records include †*Euphylax* from the Eocene of Peru, ††*Paraeuphylax* from the Miocene of Venezuela, †*Portunus* from the Miocene of Colombia, †*Johngarthia* from the Pleistocene of Brasil, ††*Falconoplax* and *Pinnixa* from the Miocene of Panamá, ††*Costacopluma*, ††*Quasilaeviranina* and ††*Palaeoxanthopsis* from the Late Cretaceous of Colombia, †*Ixa* from Chile, and some eubrachyurans from the Cenomanian of Bolivia and the Paleocene of Colombia.

Although the phylogenetic position of most brachyuran families is relatively well resolved, there are still discrepancies regarding the classification and subsequent naming of the principal brachyuran ranks above superfamily and below infraorder, i.e., sections and subsections. The International Code of Zoological Nomenclature does not regulate the nomenclature for taxa in ranks between suprafamily and infraorder, which has led to at least two different phylogenetic hypotheses: a) a monophyletic Podotremata (e.g., Guinot *et al.*, 2013; Davie *et al.*, 2015c; Jagt *et al.*, 2015), and b) a paraphyletic podotremous grade (e.g., Ahyong et al., 2007; De Grave et al., 2009; Scholtz and McLay, 2009; Karasawa et al., 2011; Tsang et al., 2014). Since the aim of the present work is to provide a revised and updated list of fossil decapod crustaceans from tropical America and not to discuss the phylogenetic relationships among higher brachyuran taxa between the superfamily and infraorder ranks, we have grouped the taxa under superfamilies, first based on their approximate phylogenetic position (e.g., typical podotremous superfamilies are listed before eubrachyuran superfamilies) (Fig. 5.2), and second, alphabetically within superfamilies. The schematic phylogenetic relationships among the Anomura and Brachyura superfamilies and sections/subsections listed in this work are partially based on the works of Bracken-Grissom *et al.* (2013) for Anomura (white box), Karasawa *et al.* (2011) for podotremous Brachyura (colored boxes), and Tsang *et al.* (2014) for eubrachyuran Brachyura (grey box) (Fig. 5.2). In this checklist, **o**ne dagger (†) denotes taxa known from fossil and extant species. Two daggers (††) indicate taxa that are exclusively known from fossils, while no daggers imply that the taxon is extinct as well as its parent genus, family, or superfamily.

5.2. Annotated checklist

Order DECAPODA † Latreille, 1802

Clade MEIURA † Saint Laurent, 1980

5.3. Northern South America

5.3.1. Bolivia

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Diogenidae *incertae sedis* [Cenomanian, Potosí] (Fig. 5.3A–H) |**Notes 1,2**|

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily ?CARPILIOIDEA † Ortmann, 1893

?**Tumidocarcinidae** †_Schweitzer, 2005b

Dynomenopsis †† Secretan, 1972

D. branisai Secretan, 1972 (type) [Cenomanian, Potosí] (Schweitzer and Feldmann, 2012) **|Note 2|**

Eubrachyura indet. 1 (carapace) [Cenomanian, Potosí] (Fig. 5.3I–J) **|Note 2|**

Eubrachyura indet. 2 (carapace) [Cenomanian, Potosí] (Fig. 5.3K–L) **|Note 2|**

Eubrachyura *incertae sedis* (claw fragments) [Cenomanian, Potosí] (Fig. 5.4A–J) **|Note 2|**

Brachyura *incertae sedis* (claw fragments) [Miocene, Santa Cruz] (Fig. 5.4K–N) [**Note 3|**

Notes

|Note 1| To date, the only known fossil decapod records from Bolivia are those reported by Secretan (1972), which included some indeterminate decapod cheliped remains, and the brachyuran *Dynomenopsis branisai*, all from the Cenomanian Miraflores Formation of the Puca Group in Esquena. A parcel of decapod remains deposited at the Paleontological Collections of the Muséum National d'Histoire Naturelle in Paris (MNHN), includes several paguroid chelipeds and many brachyuran carapace and cheliped remains (Figs 5.3–5.4). The paguroid remains consist mainly of major left chelipeds, which are characteristic of the family Diogenidae (including Coenobitinae), and reminiscent of the 'indeterminate decapod remains' reported by Secretan (1972, text fig. 1, plates II and III). Herein, we tentatively assign Secretan's specimens and the new material to Diogenidae *incertae sedis* (Fig. 5.3A–H), until further studies permit a more accurate systematic placement.

|Note 2| To our knowledge, *Dynomenopsis branisai,* from the Cenomanian of Esquena, is the only known fossil brachyuran from Bolivia to date. As suggested by Schweitzer and Feldmann (2012), the affiliation of *Dynomenopsis* with Tumidocarcinidae, or even Carpilioidea, can only be corroborated as more material becomes available. Here, we maintain it within Tumidocarcinidae albeit with uncertainty. The occurrence of two additional carapaces from apparently different taxa (Fig. 5.3I–L), increase to three the number of fossil brachyurans known from Bolivia to three. The labels and metadata associated with these specimens indicate that they were collected in Cenomanian rocks of Esquena. Several of the chelipeds and cheliped fragments here illustrated (Fig. 5.4A–J) are associated with one of the carapaces (Fig. 5.3K–L), and are strongly reminiscent of the chelipeds seen among several durophagous eubrachyurans (Luque, personal observation).

5.3.2. Brazil

Infraorder ANOMURA † MacLeay, 1838

Superfamily GALATHEOIDEA † Samouelle, 1819

Munidopsidae † Ortmann, 1898

Brazilomunida †† Martins-Neto, 2001

B. brasiliensis (Beurlen, 1965, as *Galatheites brasiiensis*) (type) [Albian, Sergipe]

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Dardanus † Paul'son, 1875

Dardanus spp. [Paleocene, Pernambuco] (in Távora *et al.*, 2005) |**Note 1**|

Infraorder BRACHYURA † Latreille, 1802

Superfamily DROMIOIDEA † De Haan, 1833

Dynomenidae † Ortmann, 1892a

Maurimia †† Martins-Neto, 2001

M. sergipensis (Beurlen, 1965, as ?*Cyclothyreus sergipensis*) (type) (as *Distefania sergipensis* in Schweitzer *et al.*, 2010) [Albian, Sergipe]

Superfamily NECROCARCINOIDEA †† Förster, 1968

Necrocarcinoidea *incertae sedis*

Araripecarcinus Martins-Neto, 1987

A. ferreirai Martins-Neto, 1987 (type) [early Albian, Ceará] |**Note 2**|

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

Raninoides spp. [Paleocene, Pernambuco] (Távora *et al.*, 2016) **[Note 3]**

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatella † Smith, 1869b

H. amazonica †† Beurlen, 1958a [early Miocene, Pará]

Calappidae † De Haan, 1833

Acanthocarpus † Stimpson, 1871

A. obscurus †† (Rathbun, 1918 [1919], as *Mursia obscura*) [early Miocene, Pará] (in Beurlen, 1958a) (Fig. 5.5A)

?*Calappa* † Weber, 1795

?*Calappa* sp. aff. *C. zurcheri* †† Bouvier, 1899 [as *Calappilia brooksi* in Távora *et al.*, 2005, and *Calappilia* in Rumsey *et al.*, 2016) [early Miocene, Pará] (Vega *et al.*, 2009)

Calappilia †† A. Milne-Edwards, 1873

C. circularis (Beurlen, 1958a, as *Calappa circularis*) [Miocene, Pará] (Fig. 5.5B)

Calappidae *incertae sedis* [early Miocene, Pará] **|Note 4|**

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Randallia † Stimpson, 1857

Randallia sp. [Miocene, Pará] (Beurlen, 1958a)

Leucosiidae *incertae sedis*

Typilobus †† Stoliczka, 1871

T. unispinatus Martins-Neto, 2001 [Miocene, Pará]

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Parthenope † Weber, 1795

P. trituberculata †† Beurlen, 1958a [Miocene, Pará]

Superfamily CANCROIDEA † Latreille, 1802

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Cyclocancer †† Beurlen, 1958a

C. tuberculatus Beurlen, 1958a (type) [Miocene, Pará]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Macropipidae † Stephenson and Campbell, 1960

Ophthalmoplax †† Rathbun, 1935b

O. brasiliana (Maury, 1930, as *Zanthopsis*) [Maastrichtian, Paraíba] (Fig. 5.5E–F)

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. tajinensis Vega, Feldmann, Villalobos-Hiriart and Gío-Argíez, 1999 (sensu Távora *et al.*, 2002) [early Miocene, Pará] **|Note 6|**

Scylla † De Haan, 1833

S. costata †† Rathbun, 1919 [Miocene, Pará] (reported in Beurlen, 1958a, and Távora *et al.*, 2002)

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. septendentatus †† Beurlen, 1958a [Miocene, Pará]

Portuninae † Rafinesque, 1815

Achelous † De Haan, 1833

A. spinimanus † (Latreille, 1819) (sensu Távora *et al.*, 2002) [early Miocene, Pará] **|Note 6|**

Arenaeus † Dana, 1851c

A. cribarius (Lamarck, 1818) [early Miocene, Pará]

Callinectes † Stimpson, 1862

C. paraensis †† Beurlen, 1958a [early Miocene, Pará] (Fig. 5.5C–D)

C. reticulatus †† Rathbun, 1918 [1919] (claws only) [early Miocene, Pará]

Portunus † Weber, 1795

P. atecuicitlis †† Vega, Feldmann, Villalobos-Hiriart and Gío-Argíez, 1999 (sensu Távora *et al.*, 2002) [early Miocene, Pará]

P. haitensis †† Rathbun, 1923b [Miocene, Pará] (sensu Távora *et al.*, 2002)

P. pirabaensis †† Martins-Neto, 2001 [Miocene, Pará]

Portunus sp. [early Miocene, Pará] (cited in Beurlen, 1958a as *Neptunus* sp., and in Távora and Dias, 2016 as *Portunus oblongus* and erroneously as *Palaeopinnixa perornata*) **|see Note 7|**

Superfamily CARPILIOIDEA † Ortmann, 1893

Palaeoxanthopsidae †† Schweitzer, 2003

Palaeoxanthopsis †† Beurlen, 1958b

P. cretacea (Rathbun, 1902) (type) [Maastrichtian, Paraiba]

Tumidocarcinidae †† Schweitzer, 2005b

Paratumidocarcinus †† Martins-Neto, 2001

P. marajoarus Martins-Neto, 2001 (type) [Miocene, Pará]

Lobonotus †† A. Milne-Edwards, 1863

L. sturgeoni (Feldmann, Bice, Schweitzer, Salva, and Pickford, 1998a) [Paleocene, Pernambuco] (in Távora *et al.*, 2005)

Superfamily RETROPLUMOIDEA † Gill, 1894

Retroplumidae † Gill, 1894

?*Archaeopus* †† Rathbun, 1908

?*A. rathbunae* Beurlen, 1965 [Albian, Sergipe] **|Note 5|**

Costacopluma †† Collins and Morris, 1975

C. nordestina Feldmann and Martins Neto, 1995 [Paleocene, Pernambuco] (Fig. 5.5G–H)

Superfamily TRICHODACTYLOIDEA † H. Milne Edwards, 1853

Trichodactylidae † H. Milne Edwards, 1853

Trichodactylidae spp. indet [late Miocene, Amazonas] (Klaus *et al.*, 2017)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Panopeus † H. Milne Edwards, 1834

P. capanemaensis †† Martins-Neto, 2001 [Miocene, Pará]

Panopeus sp. [early Miocene, Pará] (in Brito, 1971)

Tetraxanthus † Rathbun, 1898

T. rathbunae † Chace, 1939 (sensu Távora *et al.*, 2002) [Miocene, Pará]

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Johngarthia † Türkay, 1970

J. lagostoma H. Milne Edwards, 1837 (as *Gecarcinus lagostoma*) [Pleistocene, Pernambuco] (Fig. 5.6) **|Note 8|**

Sesarmidae † Dana, 1851a

Sesarma † Say, 1817

S. paraensis †† Beurlen, 1958a [Miocene, Pará]

Superfamily OCYPODOIDEA † Rafinesque, 1815

Ocypodidae † Rafinesque, 1815

Uca † Leach, 1814

U. antiqua †† Brito, 1972 (junior synonym *U. inaciobritoi* †† Martins-Neto, 2001) [Miocene, Pará] **|Note 9|**

Notes

|Note 1| Távora *et al.* (2005) reported the occurrence of the extant hermit crabs *Dardanus fucosus* Biffar and Provenzano Jr, 1972, and *D. insignis* (Saussure, 1858), from the Paleocene Maria Farinha Formation, State of Pernambuco, based on a handful of fragmentary cheliped remains. However, these ~60 million year old fossil specimens seem not to be conspecific with *D. fucosus* or *D. insignis*, and their systematic affinities need to be re-examined.

|Note 2| The holotype and sole specimen of *Araripecarcinus ferreirai* is a ventral molt, which complicates its systematic placement. Considered by Martins-Neto (1987) as a dorsal carapace of a portunid crab, Guinot and Breton (2006) recognized its superficial resemblance to raninoidan crabs. Karasawa *et al.* (2008) corroborated the raninoidan affinities. Luque (2015a) re-described and re-illustrated the type specimen of *Araripecarcinus*, and based on taxonomic and cladistics approaches, indicated that it may be closer to the necrocarcinoid-like clade of raninoidans. Furthermore, its geographic range and age also matches that of other Early Cretaceous necrocarcinoids from tropical South America (e.g., Vega *et al.*, 2010; Luque *et al.*, 2012; Karasawa *et al.*, 2014; Luque, 2014b). Although *Araripecarcinus* might be closer to Necrocarcinidae or Orithopsidae, its systematic affinities remain unclear (Luque, 2015a). The only other brachyuran remains known from the Romualdo Formation are a few zoea larvae preserved as fish stomach contents (Maisey, 1994; Maisey and Carvalho, 1995; Luque, 2015a).

|Note 3| Távora *et al.* (2016) reported a couple of specimens of *Raninoides* from the Paleocene Maria Farinha Formation that were assigned to two known fossil species from the Eocene and Oligocene of USA: *R. fulgidus* Rathbun, 1926, and *R. lewisana* Rathbun, 1926. However, the authors did not provide any discussion or remarks justifying their systematic placement. Several species of fossil *Raninoides* are known from Paleogene rocks worldwide, and most of them are difficult to tell apart from one another. Thus, based solely on the illustrations of Távora *et al.*, (2016) we cannot confirm the specific affinities of the material, and for this reason, we consider them as *Raninoides* sp. indet. until detailed comparison is made or better material becomes available.

|Note 4| Távora *et al*. (2002, fig. 8) reported a presumably indeterminate species of *Callinectes* (Portunidae) from the Miocene of Pará. Based solely on their original illustration, we conclude that the specimen does not belong to *Callinectes* or even Portunidae, but rather represents a dorsal carapace akin to Calappidae.

|Note 5| The original description of *'Archaeopus' rathbunae* does not include images of the holotype but only a single line drawing (Beurlen, 1965, fig. 4). Based exclusively on the line drawing provided by Beurlen, the specimen seems not to be congeneric with *Archaeopus*, casting doubt on its generic placement.

|Note 6| Távora *et al*. (2002) reported the occurrence of the extinct *Necronectes tajinensis* and *Scylla costata*, and the extant portunids *Achelous spinimanus*, from the lower Miocene Pirabas Formation, State of Pará, each based on one poorly preserved specimen. The sternum and only part of the chelipeds of the purported '*A. spinimanus'* are preserved, making the diagnostic characteristics of the species difficult to observe. The material of *N. tajinensis* is even less well preserved and also in ventral view, which makes the identification unreliable. Thus, we considered both records as doubtful. Likewise, the affiliation of the sole propodus of the cheliped referred to *S. costata* is dubious.

|Note 7| In a recent work, Távora and Dias (2016), report the occurrence of the swimming crab *Portunus oblongus* based on relatively poorly preserved cheliped and dorsal carapace material. Although their specimens might belong to the genus *Portunus*, their specific assignment to *P. oblongus* is not justified or discussed, especially given that at least three other species of *Portunus* – i.e., *P. atecuicitlis, P. haitensis,* and *P. pirabaensis* –, and two of its close relative *Callinectes* –i.e., *C. paraensis* and *C. reticulatus*–, are known from the same strata and age in the state of Pará. Therefore, we consider this record as *Portunus* sp. A second record assigned herein to *Portunus* sp. corresponds to what they incorrectly called *Palaeopinnixa porornata* [sic] (Távora and Dias, 2016) (correct spelling is *perornata*). *Palaeopinnixa perornata* is a crab of the family Hexapodidae –not Pinnotheridae, as suggested by the authors – characterized by the unusual reduction of their 5th pair of pereiopods and their corresponding sternite 8, giving the impression of having only three pairs of walking legs (hence Hexapodidae). Hexapodid crabs share a small and wide pea-like carapace with some Pinnotheridae due to convergence (usually no more than a couple centimeters total), which has previously influenced some authors to place fossil hexapodids among pinnotherids (Vía Boada, 1966; Collins and Rasmussen, 1992; Schweitzer and Feldmann, 2001). The large specimen illustrated by Távora and Dias (2016) as *Palaeopinnixa perornata* corresponds to the ventral carapace of a medium size Portuninae, most likely one of the *Portunus* or *Callinectes* species mentioned above. Another taxon reported by Távora and Dias (2016) was incorrectly assigned to *Piloslambrus guerini* (Parthenopidae). Despite the poor preservation and illustration of that specimen, the dorsal regions, carapace outline, and tuberculation pattern indicate that this fossil is neither conspecific nor congeneric with the extant *P. guerini.* Herein, we consider it provisionally as Eubrachyura *incertae sedis*.

|Note 8| A small lot of cheliped fragments in the USNM Paleobiology collections, collected in

1973 from “Pleistocene dune deposits at Ponto Santo Antonio, Fernando de Noronha Island, S. Atlantic Ocean (Brazil)”, is referred to the extant gecarcinid crab *Johngarthia lagostoma* (Fig. 5.6). The recent discovery of claw remains of *J. lagostoma* in Holocene deposits from the Rocas Atoll, nearby the Fernando de Noronha Island (Soares *et al.*, 2016), confirm the presence of the species in the South Atlantic Islands during the Quaternary. These occurrences represent the first fossil records of the genus (Fig. 5.6).

|Note 9| Brito (1972) named *Uca antiqua* as a subspecies of *U. maracoani* (=*U. maracoani antiqua*). Later, Martins-Neto (2001) recognized that both subspecies were different enough to merit independent species status. However, instead of elevating *antiqua* to the species level, he erected a new species, *U. inaciobritoi*, to replace it. Following Article 23.3.1. Principle of Priority of the ICZN, *Uca antiqua* Brito, 1972 is the valid name for the taxon, and *U. inaciobritoi* Martins-Neto, 2001, is thus a junior synonym, and therefore invalid. Távora (2001) synonymized *U. antiqua* with *U. maracoani* based on the study of 96 *Uca* specimens from Pirabas Formation. However, Távora (2001) did not provide characters to support his point of view. Herein, we maintain both *U. antiqua* and *U. maracoani* as valid separate species.

5.3.3. Chile

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

?Paguroidea *incertae sedis* [Maastrichtian, Algarrobo] (Schweitzer *et al.*, 2006a)

Infraorder BRACHYURA † Latreille, 1802

Superfamily HOMOLOIDEA † De Haan, 1833

Homolidae † De Haan, 1839

  Homolopsis †† Bell, 1863

    H. chilensis Förster and Stinnesbeck, 1987 [Maastrichtian, near Concepción]

Superfamily RANINOIDEA † De Haan, 1839

Lyreididae † Guinot, 1993

  Lyreidinae † Guinot, 1993

Lyreidus † De Haan, 1841

L. lebuensis †† Feldmann, 1992 [Eocene, near Lebu] (as *Lyreidus* sp. in Feldmann and Chirino-Galvez, 1991)

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

R. araucana †† (Philippi, 1887, as *Symnista araucana*) [Eocene, near Lebu]

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. spinimarginatus †† Feldmann, Schweitzer and Encinas, 2005 [Miocene, Cardenal Caro]

Calappidae † De Haan, 1833

Calappilia †† A. Milne-Edwards, 1873

?*C. chilensis* †† Feldmann, Schweitzer and Encinas, 2005 [Miocene, Cardenal Caro]

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Ixa † Leach, 1817

Ixa sp. cf. *I. cylindrus* † (Fabricius, 1777) [Cenozoic indet., locality unknown] (Fig. 5.7) |**Note 1**|

Superfamily CANCROIDEA † Latreille, 1802

Atelecyclidae † Ortmann, 1893

Trichopeltarion † A. Milne-Edwards, 1880a

T. frassinetti †† Feldmann, Schweitzer and Encinas, 2010 [late Pliocene, Guafo Island]

T. levis †† Casadío *et al.*, 2004 [Miocene, Cardenal Caro] (Feldmann *et al.*, 2005, 2010)

Superfamily CHEIRAGONOIDEA † Ortmann, 1893

Cheriagonidae † Ortmann, 1893

Pirulella †† Feldmann, Schweitzer and Encinas, 2010

P. antipodea Feldmann, Schweitzer and Encinas, 2010 [early Pliocene, Chiloé Island]

Superfamily GONEPLACOIDEA † MacLeay, 1838

Chasmocarcinidae † Serène, 1964

Chasmocarcininae † Serène, 1964

Chasmocarcinus † Rathbun, 1898

C. chiloeensis †† Feldmann, Schweitzer and Encinas, 2010 [Miocene, Chiloé Island]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Geryonidae † Colosi, 1923

Archaeogeryon †† Colosi, 1923 (= *Proterocarcinus* Feldmann, Schweitzer and Encinas, 2005)

A. navidad (Feldmann, Schweitzer and Encinas, 2005) [Miocene, Cardenal Caro] (Feldmann *et al.*, 2010)

Chaceon † Manning and Holthuis, 1989

C. quadrata †† Feldmann, Schweitzer and Encinas, 2010 [Miocene, Corrál]

Geryon † Krøyer, 1837

G. manningi † Feldmann, Schweitzer and Encinas, 2010 [early Pliocene, Chiloé Island]

Macropipidae † Stephenson and Campbell, 1960

Minohellenus †† Karasawa, 1990

M. araucanus (Philippi, 1887) [Miocene, locality indet.]

Portunidae † Rafinesque, 1815

Pheophthalmus †† Feldmann, Schweitzer, and Encinas, 2010

P. mochaensis †† Feldmann, Schweitzer and Encinas, 2010 [Miocene, Mocha Island]

Superfamily † PILUMNOIDEA Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

Pilumnus † Leach, 1816

P. cucaoensis †† Feldmann, Schweitzer and Encinas, 2005 [Miocene, Chiloé Island and Cardenal Caro] (Feldmann *et al.*, 2010)

Clade THORACOTREMATA † Guinot, 1977

Superfamily PINNOTHEROIDEA † De Haan, 1833

Pinnotheridae † De Haan, 1833

Pinnothereliinae † Alcock, 1900b

Pinnixa † White, 1846

P. navidadensis †† Feldmann, Schweitzer and Encinas, 2005 [Miocene, Cardenal Caro] (Feldmann *et al.*, 2010)

Note

|**Note 1**| This is the first occurrence of fossil *Ixa* in South America, and apparently the second record worldwide (Schweitzer *et al.*, 2010). Unfortunately, no detailed geographic or stratigraphic data is associated with the specimen here reported.

5.3.4. Colombia

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

?*Paguristes* † Dana, 1851a

?*Paguristes* sp. [late Valanginian, Santander] (Fig. 5.8A) |**Note 1**|

Infraorder BRACHYURA † Latreille, 1802

Superfamily DROMIOIDEA † De Haan, 1833

Diaulacidae †† Wright and Collins, 1972

Diaulax Bell, 1863

D. rosablanca Gómez, Bermúdez and Vega, 2015 [late Valanginian, Santander]

Diaulax sp. [late Valanginian to Albian, Santander]

Superfamily HOMOLOIDEA † De Haan, 1833

Mithracitidae †† Števčić, 2005

Mithracites Gould, 1859

M. takedai van Bakel, Guinot, Jagt and Fraaije, 2012b [late Aptian, Santander]

Superfamily NECROCARCINOIDEA †† Förster, 1968

Cenomanocarcinidae †† Guinot, Vega and van Bakel, 2008

Cenomanocarcinus Van Straelen, 1936

C. vanstraeleni Stenzel, 1945 (as *Ophthalmoplax spinosus* in Feldmann, Villamil and Kauffman, 1999; and as ?*Pinnotheres* sp. in Feldmann *et al.*, 1999) [Albian to Campanian of Cundinamarca, Boyacá and Tolima] (Vega *et al.*, 2007b; Vega *et al.*, 2010) **|Note 2|**

Orithopsidae †† Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg and Ross, 2003a

Bellcarcinus Luque, 2014b

B. aptiensis Luque, 2014b (type) [late Aptian, Santander and Boyacá] **|Note 3|**

Colombicarcinus Karasawa, Schweitzer, Feldmann and Luque, 2014

C. laevis Karasawa, Schweitzer, Feldmann and Luque, 2014 (type) [late Aptian, Santander and Boyacá] **|Note 3|**

Planocarcinus Luque, Feldmann, Schweitzer, Jaramillo and Cameron, 2012

P. olssoni (Rathbun, 1937, as *Dakoticancer olssoni*) (type) (and as *Necrocarcinus* in Feldmann *et al.*, 1999; and *Orithopsis* in Vega *et al.* 2010) [late Aptian, Santander and Boyacá] (Luque *et al.*, 2012) **|Note 3|**

P. johnjagti Bermúdez, Crúz and Vega *in* Bermúdez *et al.*, 2013 [late Aptian, Boyacá]

Superfamily PALAEOCORYSTOIDEA †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Palaeocorystidae †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Joeranina van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

J. kerri (Luque, Feldmann, Schweitzer, Jaramillo and Cameron, 2012, as *Notopocorystes kerri*) [late Aptian–middle Albian, Santander and Boyacá] (Fig. 8B)

J. colombiana Bermúdez, Crúz and Vega *in* Bermúdez *et al.*, 2013 [early–middle Albian, Boyacá]

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Quasilaeviranina †† Tucker, 1998

Quasilaeviranina sp. [early-mid Santonian to Maastrichtian, Boyacá] (Fig. 5.8C) **|Note 4|**

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily DORIPPOIDEA † MacLeay, 1838

Telamonocarcinidae †† Larghi, 2004

Telamonocarcinus Larghi, 2004

T. antiquus Luque, 2015b [early Albian, Santander] (Fig. 5.8D) **|Note 5|**

Superfamily CARPILIOIDEA † Ortmann, 1893

Palaeoxanthopsidae †† Schweitzer, 2003

Palaeoxanthopsis †† Beurlen, 1958b

Palaeoxanthopsis sp. [Maastrichtian, Santander] (Fig. 5.8E) |**Note 6**|

Superfamily PORTUNOIDEA † Rafinesque, 1815

Macropipidae † Stephenson and Campbell, 1960

Ophthalmoplax †† Rathbun, 1935b

O. andina Guzmán, Bermúdez, Gómez-Cruz and Vega 2016 [Campanian, Boyacá] |**Note 7**|

O. brasiliana (Maury, 1930) [junior synonym *O. triambonatus* Feldmann and Villamil, 2002] [Maastrichtian, Boyacá] |**Note 7**|

Portunidae † Rafinesque, 1815

Portuninae † Rafinesque, 1815

Callinectes † Stimpson, 1862

C. reticulatus †† Rathbun, 1918 [1919] (claw) [Oligocene, Antioquia]

Portunus † Weber, 1795

P. oblongus †† Rathbun, 1920b [Miocene, La Guajira] (Fig. 5.8F–G) |**Note 8**|

Superfamily RETROPLUMOIDEA † Gill, 1894

Retroplumidae † Gill, 1894

Costacopluma †† Collins and Morris, 1975

Costacopluma spp. [Coniacian to Maastrichtian of Tolima, Cundinamarca, Boyacá and Santander] (Fig. 5.8H–I) |**Note 11**|.

Superfamily TRICHODACTYLOIDEA † H. Milne Edwards, 1853

Trichodactylidae † H. Milne Edwards, 1853

Dilocarcininae † Pretzmann, 1978

Sylviocarcinus † H. Milne Edwards, 1853

S. piriformis † (Pretzmann, 1968) [early Miocene, Tolima] (Fig. 5.4B) |**Note 10**|

Eubrachyura indet. (as ?Goneplacoidea *incertae sedis,* in Kiel and Hansen, 2015) [Oligocene, Córdoba] |**Note 12**|

Eubrachyura indet. 2 [Paleocene, Guajira] (Fig. 5.8J) |**Note 13**|

Notes

|Note 1| This represents the first record of anomuran crabs from Colombia, and one of the oldest decapod crustaceans for northern South America (Fig. 5.8A). Furthermore, if its generic affinities are confirmed, this would be the earliest record for the genus, extending its temporal and spatial record from the Late Cretaceous of North America to the Early Cretaceous of northern South America (~135 Ma).

|Note 2| The species reported by Feldmann *et al.* (1999) as *Ophthalmoplax spinosus* from the Turonian of Colombia does not belong to *Ophthalmoplax* or any eubrachyuran crab. The material represents a taxon congeneric with *Cenomanocarcinus*, as suggested by Vega *et al*. (2007b). The specimen of ?*Pinnotheres* sp. in Feldmann *et al*. (1999) seems to correspond also to a poorly preserved carapace of *Cenomanocarcinus* sp.

|Note 3| *Colombicarcinus* and *Planocarcinus* share several traits with Necrocarcinidae and Orithopsidae, but the absence of ventral and appendicular characters obscures their familial affinities. A recent revision of these taxa suggests that they may represent either basal orithopsids, or even representatives of distinctive orithopsid sister clades likely related to *Bellcarcinus* and similar forms (Schweitzer *et al.*, 2016). Currently, the age of *Planocarcinus olssoni* is considered as late Aptian based on the youngest rocks outcropping near the area of collection (Luque *et al.*, 2012), in contrast to the Barremian age originally suggested by Rathbun (1937). Although it is plausible that *P. olssoni* was already present in the Barremian, the recent discovery of *P. olssoni* in the late Aptian–early Albian rocks of Boyacá in association with new records of *Bellcarcinus aptiensis* and *Joeranina kerri* (Luque, personal observation), confirms its presence during the latest Early Cretaceous (late Aptian–early Albian).

|Note 4| This is the first record of the genus *Quasilaeviranina* for tropical America, and the oldest record worldwide, i.e., early-middle Santonian (~85 Mya) given that all other quasilaeviraninids known so far are Paleocene-Eocene in age (van Bakel *et al.*, 2012a; Karasawa *et al.*, 2014; Martínez-Díaz *et al.*, 2017).

|Note 5| *Telamonocarcinus antiquus* is the oldest representative of the family Telamonocarcinidae and the superfamily Dorippoidea yet known, and together with Componocancridae Feldmann *et al.*, 2008a, and Tepexicarcinidae Luque, 2015b, represent the earliest confirmed crown-group and stem-group Eubrachyura – or higher true crabs – known to date (late Albian). Their geographic occurrences suggest that early eubrachyurans could have radiated in the Americas during the Early Cretaceous or earlier (Luque, 2015b).

|Note 6| This is the first record of the genus *Palaeoxanthopsis* and the family Palaexanthopsidae for Colombia. Its Maastrichtian age confirms the wide distribution of the genus and family in the Americas during the Late Cretaceous (Rathbun, 1902; Vega *et al.*, 2001b; Schweitzer *et al.*, 2008) (see also under 'Jamaica' herein).

|Note 7| The fossil record of *Ophthalmoplax* was recently reviewed by Vega *et al.* (2013), who recognized the morphological similarities between *O. brasiliana* and several records from Colombia and Venezuela previously reported as *O. triambonatus* Feldmann and Villamil, 2002, and currently synonymized with *O. brasiliana* (Jagt *et al.*, 2015). Recently, Guzmán *et al.* (2016) described *O. andina* from the Campanian of Colombia, being the second ophthalmoplacid species reported from Colombia. Yet, the systematic relationships among species of *Ophthalmoplax* and related genera need to be revised.

|Note 9| This is the first record of *Portunus oblongus* for Colombia; a widespread species found in Miocene rocks of Venezuela, Cuba, Dominican Republic, and Trinidad (e.g., Rathbun, 1920b; Collins and Morris, 1976; Feldmann and Schweitzer, 2004; Varela and Rojas-Consuegra, 2009; Aguilera *et al.*, 2010).

|Note 10| Fossil specimens of *Sylviocarcinus* from the Miocene Villavieja Formation of Colombia are represented solely by cheliped fragments, principally pollices, dactyli, and fragments of the palm. Rodriguez (1997) considered these fossil remains as conspecific with the extant *S. piriformis,* which today lives in the same watershed. However, it is unclear if the fossil material indeed belongs to the same species, as no carapaces have been discovered, which makes the verification of its systematic placement difficult.

|Note 11| *Costacopluma* is one of the most widespread brachyuran genera in the Cretaceous of Colombia, occurring in Coniacian to Maastrichtian rocks of Tolima, Cundinamarca, Boyacá, and Santander, and typically associated with raninids, palaeoxanthopsids, and axiidean shrimp (Luque, personal observation). These are the first reports of the genus *Costacopluma* and the family Retroplumidae for Colombia, and a detailed description of the species is forthcoming.

|Note 12| A fragmented dorsal carapace of an Oligocene brachyuran crab was assigned to ?Goneplacoidea in Kiel and Hansen (2015, fig. 5G). Investigation of the original material suggests that 1) it was illustrated upside down, and 2) that it is not a goneplacoid but may represent a xanthoid-like species (Luque, personal observation).

|Note 13| This eubrachyuran from the Cerrejón Formation in La Guajija represents the first record of Paleocene decapods in Colombia.

5.3.5. Ecuador

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

- Necronectinae † Glaessner, 1928
  - *Necronectes* †† A. Milne-Edwards, 1881b
    - *N. proavitus* †† (Rathbun, 1918 [1919]) [early Miocene, Cuenca Basin] (Morris, 1973) **|Note 1|**
- Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. oblongus †† Rathbun, 1920b [late Miocene, locality indet.] (in Collins and Morris, 1976)

Note

|Note 1| *Necronectes proavitus* is known from Miocene deposits of Ecuador, Venezuela, Panamá, Puerto Rico, and apparently Trinidad (Roberts, 1975; Feldmann *et al.*, 1993; Schweitzer *et al.*, 2002; Schweitzer *et al.*, 2006c; Collins *et al.*, 2009c; Cáceres *et al.*, 2016), which indicates a trans-isthmian distribution for the taxon. To our knowledge, this is the only record of fossil crabs from Ecuador.

5.3.6. Peru

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CANCROIDEA † Latreille, 1802

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Cancer † Linnaeus, 1758

C. borealis † Stimpson, 1862 [Miocene–early Pliocene, Pisco and Arequipa] (Fig. 5.9A–B)

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Epialtinae † MacLeay, 1838

Eoinachoides †† Van Straelen, 1933a

E. latispinosa Carriol, Muizon and Secretán, 1987 [late Miocene, Pisco] (Fig. 5.9C).

Pisinae † Dana, 1851d

Libinia † Leach, 1815

L. peruviensis †† Carriol, Muizon and Secretán, 1987 [early Pliocene, Pisco]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Geryonidae † Colosi, 1923

Chaceon † Manning and Holthuis, 1989

C. peruvianus (Orbigny, 1842, as *Portunus*) [Miocene, locality unknown] (Fig. 5.9D–E) **|Notes 1, 3|**

Portunidae † Rafinesque, 1815

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

Euphylax sp. cf. *E. callinectias* †† Rathbun, 1918 [1919] [Eocene, Pisco] (Fig. 5.9F–H) **|Notes 2, 3|**

Portununae † Rafinesque, 1815

Callinectes † Stimpson, 1862

C. ?reticulatus †† Rathbun, 1918 [1919] [middle Oligocene, Piura] (Fig 5.9I–K) **|Note 3|**

Superfamily CARPILIOIDEA † Ortmann, 1893

Zanthopsidae †† Vía Boada, 1959

Zanthopsis †† M'Coy, 1849

Z. errans Woods, 1922 [Eocene, Piura]

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. eocenica (Woods, 1922, as *Thaumastoplax*) [Eocene, Piura]

Superfamily TRICHODACTYLOIDEA † H. Milne Edwards, 1853

Trichodactylidae † H. Milne Edwards, 1853

Trichodactylidae spp. indet [middle Eocene to late Oligocene, Loreto and San Martín] (Klaus *et al.*, 2017)

Notes

|Note 1| The label associated to the holotype of *Chaceon peruvianus* (Orbigny, 1842), MNHN.F.B33420 (Fig. 5.9D–E), indicates that the specimen comes from Miocene rocks outcropping south of the Sasaco basin, likely near Nazca and Arequipa, but the precise locality or any details of its provenance are unknown (Orbigny, 1842, Part 4, T. 3, p. 107).

|Note 2| Re-examination of three specimens catalogued as ?*Callinectes* sp., i.e. USNM 618318 (one sample, Fig. 5.9F), and USNM 618319 (two samples, Fig. 5.9G–H) from the lowermost upper Eocene Basal Talara shales (*Discocyclina peruviana* zone) about a mile northwest of Lagunitas, Pisco, Peru, indicates that they belong to *Euphylax*. To our knowledge, this would represent the first record of the subfamily Podophthalminae and the genus *Euphylax* for Peru.

|Note 3| This is the first record of the subfamily Portuninae and the genus *Callinectes* for Peru (Fig. 5.9I–K). The occurrence in Peru of *Euphylax* and *Callinectes* in Eocene and Oligocene rocks, and *Cancer* and *Eoinachoides* in Miocene and Pliocene deposits (see Carriol *et al*. 1987), indicate that these genera had a wide trans-isthmian distribution during the Paleogene and Neogene.

5.3.7. Venezuela

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Paguristes † Dana, 1851a

Paguristes sp. [early Miocene, Falcón] (Aguilera *et al*., 2010)

Petrochirus † Stimpson, 1858

Petrochirus sp. [Oligo-Miocene to Pleistocene of Falcón, Lara and Sucre] (Feldmann and Schweitzer, 2004; Aguilera *et al*., 2010)

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

R. rathbunae †† Van Straelen, 1933a [late Eocene (Priabonian) to Miocene, Falcón and Lara] (Feldmann and Schweitzer, 2004; Aguilera *et al*., 2010) **|Note 1|**

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Eriosachila †† Blow and Manning, 1996

E. rathbunae (Maury, 1930) [Eocene to Miocene of Falcón, Lara and Zulia] (Van Straelen, 1933a; Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

Eriosachila sp. [early Miocene, Falcón] (Aguilera *et al.*, 2010)

Hepatella † Smith, 1869b

H. amazonica †† Beurlen, 1958a [Miocene, Falcón and Lara] (Aguilera *et al.*, 2010)

Hepatus † Latreille, 1802

H. gronovii † Holthuis, 1959 [Pleistocene, Sucre] (Aguilera *et al.*, 2010)

Hepatus sp. [early Miocene, Falcón] (In Aguilera *et al.*, 2010) |**Note 2**|

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. laraensis †† Van Straelen, 1933a [middle Eocene to early Miocene, Lara] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

C. nitida † Holthuis, 1958 [Pleistocene, Sucre] (Aguilera *et al.*, 2010)

Calappa sp. [Oligocene to early Pliocene of Falcón, Lara and Sucre] (Aguilera *et al.*, 2010) |**Note 2**|

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

P. cf. *punctata* † (Linnaeus, 1758) [Oligo-Miocene to Pleistocene of Falcón, Lara and Sucre] (Aguilera *et al.*, 2010)

Iliacantha † Stimpson, 1871

Iliacantha sp. [early to late Miocene, Falcón] (Aguilera *et al.*, 2010)

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Epialtinae † MacLeay, 1838

Eoinachoides †† Van Straelen, 1933a

E. senni Van Straelen, 1933a (type) [middle Eocene to Miocene, Falcón] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

Eoinachoides sp. [late Miocene, Falcón] (Aguilera *et al.*, 2010)

Mithracidae † MacLeay, 1838

Mithrax † Desmarest, 1823

Mithrax sp. [Plio–Pleistocene, Falcón and Sucre] (Aguilera *et al.*, 2010)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Parthenope † Weber, 1795

P. venezuelensis †† Van Straelen, 1933a [early to late Miocene (not Oligocene), Falcón] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

Parthenope sp. [early Miocene to Pliocene, Falcón and Sucre] (Aguilera *et al.*, 2010)

Platylambrus † Stimpson, 1871

Platylambrus sp. [early Miocene to Pliocene, Falcón] (Aguilera *et al.*, 2010)

Superfamily GONEPLACOIDEA † MacLeay, 1838

Chasmocarcinidae † Serène, 1964

Chasmocarcininae † Serène, 1964

Falconoplax †† Van Straelen, 1933a

F. kugleri Van Straelen, 1933a (type) [middle-late Eocene to early Miocene, Lara and Falcón] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. perornata Collins and Morris, 1976 [early Miocene (not Oligocene), Falcón and Lara] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010) (Fig. 5.10J–M) |**Note 3**|

Superfamily PORTUNOIDEA † Rafinesque, 1815

Macropipidae † Stephenson and Campbell, 1960

Ophthalmoplax †† Rathbun, 1935b

O. brasiliana (Maury, 1930 [junior synonym *O. triambonatus* Feldmann and Villamil, 2002]) [Maastrichtian, Táchira] (in Aguilera *et al.*, 2010)

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. proavitus †† (Rathbun, 1918 [1919]) [late Miocene, Falcón) (Cáceres *et al.*, 2016)

?*Necronectes* sp. [Miocene, Lara] (Aguilera *et al.*, 2010) |**Note 2|**

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

Euphylax sp. [Miocene to Pliocene, Falcón and Zulia]

Paraeuphylax †† Varela and Schweitzer, 2011

P. cubaensis Varela and Schweitzer, 2011 [early Miocene, Zulia] (Fig. 5.10I) |**Note 4**|

?*Saratunus* †† Collins, Lee and Noad, 2003

?*Saratunus* sp. [early Miocene, Falcón] (Aguilera *et al.*, 2010) |**Note 2|**

Portuninae † Rafinesque, 1815

Callinectes † Stimpson, 1862

C. reticulatus †† Rathbun, 1918 [1919] (claws only) [early Miocene, Zulia] (Fig. 5.10E–F)

Callinectes sp. cf. *C. declivis* †† Rathbun, 1918 [1919] [Miocene, Zulia] (Fig. 5.10G–H)

Portunus † Weber, 1795

P. gibbesii † (Stimpson, 1862) [Miocene to Pleistocene, Falcón and Sucre] (Aguilera *et al.*, 2010)

P. oblongus †† Rathbun, 1920b [Miocene, Falcón and Lara] (Feldmann and Schweitzer, 2004; Aguilera *et al.*, 2010)

Portunus sp. [early Miocene to Pliocene, Falcón] (Aguilera *et al.*, 2010)

Scylla † De Haan, 1833

Scylla sp. [Miocene to Pliocene, Falcón and Lara] (Aguilera *et al.*, 2010) |**Note 2|**

Superfamily RETROPLUMOIDEA † Gill, 1894

Retroplumidae † Gill, 1894

Costacopluma †† Collins and Morris, 1975

C. bifida Collins, Higgs and Cortitula, 1994 [Paleocene, Zulia]

Costacopluma sp. [Paleocene, Trujillo] (Aguilera *et al.*, 2010) |**Note 2|**

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurytium † Stimpson, 1859

Eurytium sp. [Pliocene, Falcón] (Aguilera *et al.*, 2010)

Notes

|Note 1| Feldmann and Schweitzer (2004) commented that the association of *Raninoides rathbunae* with taxa like *Eriosachila* and *Falconoplax* suggests a Miocene age for the assemblage, thus casting doubts on its Eocene age. We concur. However, we tentatively maintain the stratigraphic record of *R. rathbunae* as ?Eocene – Miocene until new material with clearer stratigraphic information becomes available.

|Note 2| Unidentified cheliped remains by Aguilera *et al.* (2010) have been tentatively assigned to *Scylla* sp. [Miocene], ?*Necronectes* [Miocene] and doubtfully *Saratunus* [Miocene]. The presence of *Necronectes* in Venezuela has been recently confirmed (Cáceres *et al.*, 2016). *Scylla* is known from Puerto Rico and Brazil, so its occurrence in Venezuela and other countries in tropical America would not be unexpected. Aguilera *et al.* (2010) also report the occurrence of indeterminate species of *Calappa* [Miocene to Pleistocene], *Hepatus* [Miocene], and *Costacopluma* [Paleocene]; all three known from other Venezuelan localities of similar age.

|Note 3| A specimen of *Palaeopinnixa perornata* herein illustrated (Fig. 5.10J–K) has a circular hole over the left branchial region of the carapace. It superficially resembles a predatory drill hole (see Klompmaker *et al.*, 2013b), but it is more circular than bacterial lesions (Klompmaker *et al.*, 2016a). Additional study is needed to check whether the hole penetrates part of the cuticle or only the internal mold.

|Note 4| A specimen in the USNM Paleobiology collections from the early Miocene of the Zulia State, is herein assigned to *Paraeuphylax cubaensis* (Fig. 5.10I). *Paraeuphylax* superficially resembles *Saratunus* and *Euphylax*; two genera previously reported from the Miocene of Falcón and the Pliocene San Gregorio Formation, Venezuela (Aguilera *et al.* 2010). However, *Paraeuphylax* differs from these genera by its wider carapace, wider orbits (nearly one-third the carapace width), narrower rostrum (one-tenth the carapace width), and the presence of eight anterolateral spines excluding the outer orbital one (Collins *et al.*, 2003; Varela and Schweitzer, 2011).

5.4. Central America and southern North America

5.4.1. Belize

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily PORTUNOIDEA † Rafinesque, 1815

Carcineretidae †† Beurlen, 1930

Carcineretes †† Withers, 1922

C. planetarius Vega, Feldmann, Ocampo and Pope, 1997 [Maastrichtian, Albion Island]

5.4.2. Costa Rica

Infraorder ANOMURA † MacLeay, 1838

Superfamily GALATHEOIDEA † Samouelle, 1819

Porcellanidae † Haworth, 1825

Pachycheles † Stimpson, 1858

P. latus †† Rathbun, 1918 [1919] [Pliocene, Port Limón] (Fig.5.11A)

Petrolisthes † Stimpson, 1858

P. avitus †† Rathbun, 1918 [1919] [Pliocene, Port Limón] (Fig. 5.11.1B)

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

Raninoides sp. cf. *R. benedicti* † Rathbun, 1935a [?early Pleistocene, Burica Peninsula]

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. lineatinus †† Collins and Todd *in* Todd and Collins, 2005 [late Pliocene to early Pleistocene, Puntarenas)

H. biformis †† Collins *in* Todd and Collins, 2005 [early Pliocene, Puntarenas]

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. costaricana †† Rathbun, 1918 [1919] [Pliocene; Puerto Limón] (Todd and Collins, 2005)

Cryptosoma † Brullé, 1839

C. bairdii † (Stimpson, 1862) [early Pleistocene, Puntarenas] (Todd and Collins, 2005)

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Leucosilia † Bell, 1855

L. bananensis †† Rathbun, 1918 [1919] [Pliocene, Limón)] (Todd and Collins, 2005)

Speleophorus † A. Milne-Edwards, 1865

S. ?subcircularis †† Collins and Todd *in* Todd and Collins, 2005 [early Pleistocene, Puntarenas] (Todd and Collins, 2005)

Persephona † Leach, 1817

Persephona sp. cf. *P. enigmatica* Collins and Todd *in* Todd and Collins, 2005 [late Pliocene, Limón]

Persephona sp. [Limón, Puntarenas] (Todd and Collins, 2005)

Superfamily MAJOIDEA † Samouelle, 1819

Mithracidae † MacLeay, 1838

Thoe † Bell, 1836

T. asperoides †† Collins and Todd *in* Todd and Collins, 2005 [late Pliocene to early Pleistocene, Limón]

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Platylambrus † Stimpson, 1871

P. spinulatus †† Collins and Todd *in* Todd and Collins, 2005 [early Pleistocene, Limón]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. callinectias †† Rathbun, 1918 [1919] [early Pliocene (not Miocene), Limón] (Todd and Collins, 2005)

E. fortis †† Rathbun, 1918 [1919] [early Pliocene (not Miocene), Limón] (Todd and Collins, 2005)

E. maculatus †† Collins and Todd *in* Todd and Collins, 2005 (claw fragments) [early Pleistocene, Puntarenas]

Sandomingia †† Rathbun, 1919

S. yaquiensis Rathbun, 1919 [late Pliocene, Limón]

Portuninae Rafinesque, 1815

Callinectes † Stimpson, 1862

C. declivis †† Rathbun, 1918 [1919] (fingers only) [early Pliocene to early Pleistocene, Limón] (Todd and Collins, 2005)

Portunus † Weber, 1795

P. gabbi †† Rathbun, 1919 [Pliocene, Limón]

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Lophopanopeus † Rathbun, 1898

L. maculoides †† Collins and Todd *in* Todd and Collins, 2005 [late Pliocene, Limón]

Xanthidae † MacLeay, 1838

Actaeinae † Alcock, 1898

Heteractaea † Lockington, 1877

H. lunata †† (Milne Edwards and Lucas, 1843) [late Pliocene to early Pleistocene, Limón]

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

C. guanhumi † Latreille, 1828 [late Pliocene to early Pleistocene, Limón]

5.4.3. Honduras

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

Clade THORACOTREMATA † Guinot, 1977

Superfamily OCYPODOIDEA † Rafinesque, 1815

Ocypodidae † Rafinesque, 1815

Uca † Leach, 1814

Uca sp. aff. *U. ornata* or *U. insignis* (as U. *'marinae'* Domínguez Alonso, 2008) [Plio–Pleistocene, Choluteca] |**Note 1**|

Note

|**Note 1**| Following the work of Dominguez (2008), Luque *et al.* (in press) found that the Honduras material seems to be close to *U. ornata*, except for the similarity between the ornamentation on the merus of the major claw of some male *U. 'marinae'* and male *U. insignis*. However, the Honduras material differs from *U. insignis* in several aspects, which it shares in common with extant and fossil *U. ornata.* Alternatively, since *U. ornata* and *U. insignis* can be found in sympatry today, it is possible that the Honduras fossil assemblage might comprise individuals from both species (Luque *et al.*, in press).

5.4.4. Panama

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Dardanus † Paul'son, 1875

D. biordines †† Collins and Todd *in* Todd and Collins, 2005 [early Pliocene, Bocas del Toro]

Petrochirus † Stimpson, 1858

P. bouvieri †† Rathbun, 1918 [1919] [late Miocene to late Pliocene, Bocas del Toro, Colón and Darién]

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Ranininae † De Haan, 1839

?*Ranina* † Lamarck, 1801

?*Ranina* sp. [Miocene, Chiriquí]

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

Raninoides sp. cf. *R. benedicti* † Rathbun, 1935a [late Miocene of Bocas del Toro, Chiriquí and Colón] (Fig. 5.11C–D)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Eriosachila †† Blow and Manning, 1996

E. terryi †† (Rathbun, 1937, as *Zanthopsis terryi*) [late Eocene, Panamá]

Hepatus † Latreille, 1802

H. biformis †† Collins and Todd *in* Todd and Collins, 2005 [late Miocene, Bocas del Toro]

H. chiliensis † H. Milne Edwards, 1837 [Pleistocene, Panamá Canal Zone]

H. lineatinus †† Collins and Todd *in* Todd and Collins, 2005 [middle Miocene to late Pliocene, Bocas del Toro and Colón]

Hepatus sp. [middle Holocene, Bahía de Panamá] (Portell *et al.*, 2012; Klompmaker *et al.*, 2016b; Luque *et al.*, in press)

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. flammea † (Herbst, 1794) [late Miocene to Pleistocene, Colón]

C. zurcheri †† Bouvier, 1899 [Miocene, unknown provenance] (Fig. 5.12M) |**Note 1**|

Calappa sp. [early Late Pliocene, Bocas del Toro] (in Todd and Collins, 2005)

Calappella †† Rathbun, 1918 [1919]

C. quadrispina Rathbun, 1918 [1919] (type) [early Miocene (not Oligocene), Panamá Canal]

Cryptosoma † Brullé, 1839

C. bairdii † (Stimpson, 1862) [early late Pliocene, Bocas del Toro] (in Todd and Collins, 2005)

Mursia † Desmarest, 1823

M. macdonaldi †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal]

M. obscura †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal]

Mursilia †† Rathbun, 1918 [1919]

M. ecristata †† Rathbun, 1918 [1919] [early to middle Miocene, Colón]

Superfamily CANCROIDEA † Latreille, 1802

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Cancer † Latreille, 1802

C. santosi †† (Rathbun, 1937, as *Lobocarcinus santosi*) [late Eocene, Los Santos]

Cheiragonidae † Ortmann, 1893

Montezumella †† Rathbun, 1930

M. casayetensis †† Rathbun, 1937 [late Oligocene or early Miocene, Panamá Bay]

Superfamily DORIPPOIDEA † MacLeay, 1838

?Goniochelidae †† Schweitzer and Feldmann, 2011b

?*Goniochele* †† Bell, 1858

?*G. armata* †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal] (Fig. 5.11E) |**Note 2|**

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Iliacantha † Stimpson, 1871

I. panamica †† Collins and Todd *in* Todd and Collins, 2005 [late Miocene, Bocas del Toro]

Iliacantha sp. [early late Pliocene, Bocas del Toro] (Todd and Collins, 2005)

Leucosilia † Bell, 1855

L. bananensis †† Rathbun, 1918 [1919] [middle-late Miocene, Bocas del Toro and Colón]

L. jurinii † (Saussure, 1853), [Pleistocene, Colón] (Rathbun, 1918 [1919])

Leucosilia sp. cf. *L. jurini*. [Quaternary, Bahía de Panamá] (Luque *et al.*, 2017a)

Persephona † Leach, 1817

P. enigmatica †† Collins and Todd *in* Todd and Collins, 2005 [early late Pliocene, Bocas del Toro]

P. manningi †† Collins and Todd *in* Todd and Collins, 2005 [early late Pliocene, Bocas del Toro]

Speloeophorus † A. Milne-Edwards, 1865

S. subcircularis †† Collins and Todd *in* Todd and Collins, 2005 [early late Pliocene, Bocas del Toro]

Superfamily MAJOIDEA † Samouelle, 1819

Mithracidae † MacLeay, 1838

Thoe † Bell, 1836

T. asperoides †† Collins and Todd *in* Todd and Collins, 2005 [late Miocene, Bocas del Toro]

Oregoniidae † Garth, 1958

Hyas † Leach, 1814 [in Leach, 1813–1815]

Hyas sp. [late Miocene, Darién] (Todd and Collins, 2005)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Parthenope † Weber, 1795

P. panamensis †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal]

P. pleistocenica †† Rathbun, 1918 [1919] [Pleistocene, Colón]

Platylambrus † Stimpson, 1871

P. spinulatus †† Collins and Todd *in* Todd and Collins, 2005 [early late Pliocene, Bocas del Toro]

Superfamily GONEPLACOIDEA † MacLeay, 1838

Chasmocarcinidae † Serène, 1964

Chasmocarcininae † Serène, 1964

Falconoplax †† Van Straelen, 1933a

F. kugleri Van Straelen, 1933a [early Miocene, Panamá Canal] (Fig. 5.11J–Q) **|Note 3|**

Euryplacidae † Stimpson, 1871

Euryplax † Stimpson, 1859

?*E. culebrensis* †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal] (Fig. 5.11F) **|Note 4|**

Euryplax sp. [early Miocene, Panamá Canal] (Fig. 5.11G–I) **|Note 4|**

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. prima (Rathbun, 1918 [1919], as *Thaumastoplax prima*) [early Miocene (not Oligocene), Panamá Canal] (Fig. 5.12A–L) **|Note 5|**

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. proavitus †† (Rathbun, 1918 [1919], as *Gatunia proavita*) [early Miocene, Colón] (Fig. 5.12N)

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. callinectias †† Rathbun, 1918 [1919] [early Miocene (not Oligocene), Panamá Canal]

E. maculatus †† Collins and Todd *in* Todd and Collins, 2005 [middle-late Miocene to early late Pliocene, Bocas del Toro, Colón and Darién]

Euphylax sp. [Quaternary, Panama Province (dredged)] (Fig. 5.12 N-O)

Sandomingia †† Rathbun, 1919

S. yaquiensis Rathbun, 1919 [early to late Pliocene, Bocas del Toro]

Portuninae † Rafinesque, 1815

Callinectes † Stimpson, 1862

C. declivis †† Rathbun, 1918 [1919] [late Eocene to early Miocene, Panamá Canal]

C. reticulatus †† Rathbun, 1918 [1919] [early Miocene, Panamá Canal]

Callinectes sp. cf. *C. arcuatus* † Ordway, 1863 [Quaternary, Bahía de Panamá] (Portell *et al.*, 2012; Luque *et al.*, in press)

Portunus † Weber, 1795

P. gabbi †† Rathbun, 1919 [middle-late Miocene, Darién]

Portunus sp. cf. *P. tenuis* †† Rathbun, 1919 [Pleistocene, Chiriquí] **|Note 6|**

Superfamily ERIPHIOIDEA † MacLeay, 1838

Eriphiidae † MacLeay, 1838

Eriphia † Latreille, 1817

Eriphia sp. aff. *E. squamata* Stimpson, 1859 [Quaternary, Bahía de Panamá] (Luque *et al.*, in press)

Platyxanthidae † Guinot, 1977

Platyxanthus † A. Milne-Edwards, 1863

Platyxanthus sp. [late Miocene, Bocas del Toro] (in Todd and Collins, 2005)

Superfamily † PILUMNOIDEA Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

Pilumnus † Leach, 1816

Pilumnus sp. [Pliocene- early Pleistocene, Bocas del Toro and Chiriquí] (in Todd and Collins, 2005)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurytium † Stimpson, 1859

E. crenulatum †† Rathbun, 1918 [1919] [Pleistocene, Colón] |**Note 7**|

Panopeus † H. Milne Edwards, 1834

P. antepurpureus †† Rathbun, 1918 [1919] [Pleistocene, Colón and Darién]

P. chilensis † Milne Edwards and Lucas, 1843 (claw fragment) [?early Pleistocene, Bocas del Toro] (in Todd and Collins, 2005)

Xanthidae † MacLeay, 1838

Actaeinae † Alcock, 1898

Heteractaea † Lockington, 1877

H. lunata †† (H. Milne Edwards and Lucas, 1843) [late Pliocene, Bocas del Toro]

Xanthinae † MacLeay, 1838

Micropanope † Stimpson, 1871

Micropanope sp. [early late Pliocene, Bocas del Toro] (in Todd and Collins, 2005)

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

C. crassum † Smith, 1870 [Quaternary, Bahía de Panamá] (Portell *et al.*, 2012; Luque *et al.*, in press) |**Note 8**|

Grapsidae † MacLeay, 1838

Grapsus Lamarck, 1801

Grapsus sp. aff. *G. grapsus* (Linnaeus, 1758) [Quaternary, Bahía de Panamá] (Portell *et al.*, 2012; Luque *et al.*, in press) **|Note 8|**

Superfamily OCYPODOIDEA † Rafinesque, 1815

Ocypodidae † Rafinesque, 1815

Ocypodinae † Rafinesque, 1815

Uca † Leach, 1814

U. ornata † Smith, 1870 [Quaternary, Bahía de Panamá] (Portell *et al.*, 2012; Luque *et al.*, in press) **|Note 9|**

Uca sp. [as *U. macrodactyla* in Rathbun, 1918 [1919]) **|Note 9|**

Superfamily PINNOTHEROIDEA † De Haan, 1833

Pinnotheridae † De Haan, 1833

Pinnothereliinae † Alcock, 1900b

Pinnixa † White, 1846

Pinnixa sp. [early Miocene, Panama Canal (Fig. 5.12Q) **|Note 10|**

Notes

|Note 1| *Calappa zurcheri* is the first described fossil decapod crustacean from Panama. Although Bouvier (1899) reported it as Miocene in age, its exact geographic provenance and stratigraphic context is unknown. Based on our own field observations and the stratigraphic context of recent findings, Bouvier's specimen could come from the early excavations of the Panama Canal, as we have recovered similar material from the Miocene Culebra and Gatún formations in the area of the ongoing expansion of the Canal.

|Note 2| *Goniochele* is the type genus of Goniochelidae, a monotypic eubrachyuran family apparently akin with Dorippoidea (Schweitzer and Feldmann, 2011b; Guinot *et al.*, 2013; Luque, 2015b). Its confirmed fossil record is restricted to two species from the Eocene of Europe: *G. angulata* Bell, 1858, and *G. madseni* Collins and Jakobsen, 2003. A putative third species, *G. armata* Rathbun, 1918[1919] (Fig. 5.11E), was originally described from the Miocene (not

Oligocene) Culebra Formation from the Panama Canal based on the isolated dactylus of a left cheliped. The general elongate triangular shape with armed edges suggested to Rathbun (1918[1919]) affinities with *Goniochele*. Due to the lack of additional material from the Panama Canal, it is hard to confirm Rathbun's dactylus with *Goniochele*, thus we maintain it in the genus but with uncertainty.

|Note 3| Despite being one of the most abundant crabs from the Miocene Culebra Formation (hundreds of specimens), the works by Robins *et al.* (2016) and the present checklist are the first reports of *Falconoplax* for Panamá (Fig. 5.11J–Q).

|Note 4| As noted by Collins *et al*. (2009c), Rathbun (1918 [1919]) erected several new genera and species based on fragmentary material, including isolated pollices and dactyli. *Euryplax culebrensis* seems not to be an exception. The only goneplacoid crabs clearly known from the fossil record of Panama are the abundant *Palaeopinnixa prima* and *Falconoplax kugleri*. Both taxa are represented by hundreds of specimens (Robins *et al.*, 2016), often so complete that the appendages are still attached to the body as in life position. The holotype of *Euryplax culebrensis* may therefore represent cheliped material from either *P. prima* or *F. kugleri.*

|Note 5| *Palaeopinnixa prima* is similar in shape to the coeval *P. perornata* from Venezuela, but differs in the carapace outline, the latter having more roundish lateral margins. *Palaeopinnixa* is, together with *Falconoplax*, the most abundant crab in the Culebra Formation (Robins *et al.*, 2016).

|Note 6| The material of *Portunus tenuis* reported by Rathbun (1918 [1919]) and Todd and Collins (2005) consist of cheliped fragments, making its systematic placement questionable.

|Note 7| *Eurytium crenulatum* was described by Rathbun (1918 [1919]), based on a right dactylus found in Pleistocene sediments near Mount Hope in the Colón Province, Panama. Additional carapace and cheliped material from lower to upper Pliocene rocks of the Limón Province, Costa Rica, has been assigned to *E. crenulatum* since then (Todd and Collins, 2005; Collins *et al.*, 2009c).

|Note 8| The occurrences of the land crab *Cardisoma crassum* and the Sally Lightfoot crab *Grapsus grapsus* in the Quaternary of the Pacific Coast of Panama represent the first and second known fossil records of these species to date, respectively (Luque *et al.*, 2015; Luque *et al.*, in press).

|Note 9| This mid-Holocene occurrence of *Uca ornata* accounts for the most complete and abundant fiddler crab fossil record known, constituted by several hundred specimens of juveniles and adults from both sexes (Luque *et al.*, in press). Another fossil fiddler crab from Panama is *Uca macrodactyla* Rathbun, 1918 [1919], described based on a single dactylus of an ambulatory leg from Pleistocene deposits near Colón. Crane (1975) commented about the uncertain specific affinities of Rathbun's fossil, and also the synonymy of *U. macrodactyla* with *U. galapagensis* s.l. We concur with Crane (1975), and consider the specimen as an indeterminate species of *Uca* s.l.

|Note 10| This is the first report of fossil pinnotherids from Panama, and the second record of the genus *Pinnixa* for the Americas, with *P. navidadensis* from the Miocene of Chile representing the only other record known thus far.

5.4.5. Mexico

Infraorder ANOMURA † MacLeay, 1838

Superfamily AEGLOIDEA † Dana, 1852

Aeglidae † Dana, 1852

Protaegla †† Feldmann, Vega, Applegate and Bishop, 1998b

P. miniscula Feldmann, Vega, Applegate and Bishop, 1998b [Albian, Puebla] (Vega *et al.*,

2005) (Fig. 5.13A)

Superfamily GALATHEOIDEA † Samouelle, 1819

Galatheidae † Samouelle, 1819

Galatheidae indet. [middle Eocene, Baja California Sur] (Schweitzer *et al.*, 2006b)

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

?*Paguristes* † Paul'son, 1875

?*P. mexicanus* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a [middle Eocene, Chiapas, Baja California Sur] (Schweitzer *et al.*, 2002; Schweitzer *et al.*, 2005; Vega *et al.*, 2008)

Petrochirus † Stimpson, 1858

Petrochirus sp. [middle Eocene and early Miocene, Chiapas] (Vega *et al.*, 2008; Vega *et al.*, 2009)

Paguridae † Latreille, 1802

Pagurus † Fabricius, 1775

Pagurus sp. [Albian, Puebla] (Vega *et al.*, 2005)

Palaeopagurus †† Van Straelen, 1925

Palaeopagurus sp. cf. *P. pilsbyi* Roberts, 1962 [early Maastrichtian, Nuevo León] (Vega *et al.*, 1995b)

Paguroidea spp. indet. [middle Eocene, Baja California Sur] (see Schweitzer *et al.*, 2005)

Infraorder BRACHYURA † Latreille, 1802

Superfamily DROMIOIDEA † De Haan, 1833

Dynomenidae † Ortmann, 1892a

Graptocarcinus †† Roemer, 1887

G. muiri Stenzel, 1944a [Albian, San Luis Potosí]

Xandarocarcinidae †† Karasawa Schweitzer and Feldmann, 2011

Xandarocarcinus Karasawa, Schweitzer and Feldmann, 2011 (as *Xandaros* in Bishop, 1988)

X. sternbergi (Rathbun, 1926) [Maastrichtian, Baja Calafornia Sur] (Bishop, 1986; Schweitzer et al., 2002)

Dromioidea *incertae sedis*

Prehepatus †† Rathbun, 1935b

P. harrisi Bishop, 1985 [early Maastrichtian, Nuevo León] (Vega *et al.*, 1995b)

P. mexicanus Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

Superfamily HOMOLOIDEA † De Haan, 1833

Homolidae † De Haan, 1839

Homola † Leach, 1816 [imprint 1815]

H. bajaensis †† Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

Zygastrocarcinus †† Bishop, 1983a

Z. carolinasensis Klompmaker, Flores-Ventura and Vega, 2013a [late Campanian, Coahuila] (Vega *et al.*, 2016)

Superfamily NECROCARCINOIDEA †† Förster, 1968

Cenomanocarcinidae †† Guinot, Vega and van Bakel, 2008

Cenomanocarcinus Van Straelen, 1936

C. vanstraeleni Stenzel, 1945 [Turonian-Coniacian, Coahuila] (Vega *et al.*, 2007b; Vega *et al.*, 2010; Garassino *et al.*, 2013) (Fig. 5.13B)

Cenomanocarcinus sp. [Campanian, Guerrero] (in Vega *et al.*, 2010)

Superfamily PALAEOCORYSTOIDEA †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Palaeocorystidae †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Ferroranina †† van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

Ferroranina sp. cf. *F. dichrous* (Stenzel, 1945) [Turonian, Coahuila] (Vega *et al.*, 2007b)

Superfamily RANINOIDEA † De Haan, 1839

Lyreididae † Guinot, 1993

Macroacaeninae Karasawa, Schweitzer, Feldmann and Luque, 2014

Macroacaena †† Tucker, 1998

M. venturai Vega, Nyborg, Fraaye and Espinosa, 2007a [Paleocene (Selandian), Coahuila]

Marylyreidinae †† van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

Bournelyreidus van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

B. oaheensis (Bishop, 1978) [early Maastrichtian, Coahuila] (Vega *et al.*, 2016)

Raninidae † De Haan, 1839

Cyrtorhininae † Guinot, 1993

Claudioranina †† Karasawa, Schweitzer, Feldmann and Luque, 2014

C. latacantha Martínez, Aguillón, Luque and Vega, 2017 [Paleocene (Selandian), Coahuila]

Notopodinae † Serène and Umali, 1972

Notopus † De Haan, 1841

N. minutus †† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a [Ypresian, Chiapas]

Ranininae † De Haan, 1839

Lophoranina †† Fabiani, 1910

L. bishopi Squires and Demetrion, 1992 [Ypresian and Eocene indet., Baja California, Sur] (Schweitzer *et al.*, 2002; Schweitzer *et al.*, 2007b)

L. cristaspina Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a [middle Eocene and Ypresian, Baja California Sur; Ypresian, Chiapas] (Hernández-Monzón *et al.*, 2007; Vega *et al.*, 2008) (Fig. 5.13C)

?*Ranina* † Lamarck, 1801

?*R. berglundi* †† Squires and Demetrion, 1992 [middle Eocene and Ypresian, Baja California Sur] (Schweitzer *et al.*, 2006b; Vega *et al.*, 2008; Pasini and Garassino, 2017)

?*Ranina* sp. [Eocene, Baja California Sur] (Rathbun, 1930)

Vegaranina †† van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

V. precocia (Feldmann, Vega, Tucker, García-Barrera and Avendaño, 1996, as *Lophoranina precocious*) (type) [Maastrichtian, Chiapas]

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Notopoides † Henderson, 1888

N. exiguus †† Beschin, Busulini, De Angeli and Tessier, 1998 [Ypresian, Chiapas] (Vega *et al.*, 2008)

Notopoides sp. [Paleocene (Selandian), Coahuila] (Martínez-Díaz *et al.*, 2017)

Quasilaeviranina †† Tucker, 1998

Quasilaeviranina sp. cf. *arzignanensis* (Beschin, Busulini, De Angeli & Tessier, 1998) [Paleocene (Selandian), Coahuila] (Martínez-Díaz *et al.*, 2017)

Quasilaeviranina sp. cf. *ovalis* (Rathbun, 1935b) [Paleocene (Selandian), Coahuila] (Martínez-Díaz *et al.*, 2017)

Raninoides † H. Milne Edwards, 1837

R. acanthocolus †† Schweitzer, Feldmann, Gonzalez-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

R. mexicanus †† Rathbun, 1930 [Miocene, Veracruz]

R. proracanthus †† Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

R. treldenaesensis †† Collins and Jakobsen, 2003 [Ypresian, Chiapas] (Vega *et al.*, 2008)

Raninidae spp. indet. [Turonian, Coahuila] (Vega *et al.*, 2007b)

Section DAKOTICANCROIDA †† Rathbun, 1917

Superfamily DAKOTICANCROIDEA † Rathbun, 1917

Dakoticancridae †† Rathbun, 1917

Dakoticancer †† Rathbun, 1917

D. australis Rathbun, 1935b [early Maastrichtian, San Luis Potosí and Nuevo León] (Vega and Feldmann, 1991; Vega *et al.*, 1995a; Vega *et al.*, 2016)

Ibericancridae †† Artal, Guinot, van Bakel and Castillo, 2008

?*Sodakus* †† Bishop, 1978

S. mexicanus Vega, Feldmann and Villalobos-Hiriart, 1995b [early Maastrichtian, Nuevo León and Coahuila] (Vega *et al.*, 2016) (Fig. 5.13D)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily ?DORIPPOIDEA † MacLeay, 1838

Tepexicarcinidae †† Luque, 2015b

Tepexicarcinus †† Feldmann, Vega, Applegate and Bishop, 1998b

T. tlayuaensis Feldmann, Vega, Applegate and Bishop, 1998b [Albian, Puebla] (Vega *et al.*, 2005) (Fig. 5.13E)

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Eriosachila †† Blow and Manning, 1996

E. bajaensis Schweitzer, Feldmann, González-Barba and Vega, 2002 [Eocene (Bartonian), Baja California Sur] (Schweitzer *et al.*, 2007a)

Eriosachila sp. [middle Eocene, Chiapas] (Vega *et al.*, 2001a)

Hepatella † Smith, 1869b

H. amazonica †† Beurlen, 1958a [early Miocene, Chiapas] (Vega *et al.*, 2009)

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. flammea † (Herbst, 1794) [Oligocene, Baja California Sur] (Rathbun, 1930)

C. zurcheri †† Bouvier, 1899 [Oligocene, Veracruz; early Miocene, Chiapas] (Rathbun, 1930; Vega *et al.*, 2009)

Calappilia †† A. Milne-Edwards, 1873

C. hondoensis Rathbun, 1930 [middle Eocene: Lutetian, Chiapas; Priabonian, Baja California Sur] (Vega *et al.*, 2001a; Schweitzer *et al.*, 2006b; Schweitzer *et al.*, 2007a; Vega *et al.*, 2008

Mursia † Leach *in* Desmarest, 1823

?*Mursia* sp. [middle Miocene, Veracruz] (Vega *et al.*, 1999)

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Iliacantha † Stimpson, 1871

I. panamanica †† Collins and Todd *in* Todd and Collins, 2005 [early Miocene, Chiapas] (Vega *et al.*, 2009)

Superfamily MAJOIDEA † Samouelle, 1819

Oregoniidae † Garth, 1958

Oregonia † Dana, 1851b

O. spinifera †† Schweitzer, Feldmann, González-Barba and Vega, 2002 [Oligocene, Baja California Sur]

Majidae † Samouelle, 1819

?Majidae indet. [Maastrichtian, San Luis Potosí] (Vega *et al.*, 1995a)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Daldorfiinae † Ng and Rodríguez, 1986

Daldorfia † Rathbun, 1904

D. salina †† Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

Superfamily GONEPLACOIDEA † MacLeay, 1838

Euryplacidae † Stimpson, 1871

Orbitoplax †† Tucker and Feldmann, 1990

O. nandachare (Vega *et al.*, 2001a, as *Stoaplax nandachare*) [Ypresian, Chiapas] (Vega *et al.*, 2008)

Goneplacidae† MacLeay, 1838

Amydrocarcinus †† Schweitzer, Feldmann, González-Barba and Vega, 2002

A. dantei Schweitzer, Feldmann, González-Barba and Vega, 2002 [Eocene (Bartonian), Baja California Sur] (Schweitzer *et al.*, 2007a)

Litocheiridae † Števčić, 2005

Paracorallicarcinus †† Tessier, Beschin, Bussulini and De Angeli, 1999

P. tricarinatus Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

Mathildellidae † Karasawa and Kato, 2003

Tehuacana †† Stenzel, 1944b

T. americana (Stenzel, 1944b) [Paleocene (Selandian), Coahuila] (Vega *et al.*, 2007a; Vega *et al.*, 2008; Armstrong *et al.*, 2009; Martínez-Díaz *et al.*, 2017)

T. schweitzerae Vega, Nyborg, Coutiño and Hernández-Monzón, 2008 [Eocene (Lutetian), Chiapas]

Mathildellidae indet. [late Campanian, Coahuila] (Vega *et al.*, 2016)

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. perornata Collins and Morris, 1976 [early Miocene, Chiapas] (Vega *et al.*, 2009)

Superfamily RETROPLUMOIDEA † Gill, 1894

Retroplumidae † Gill, 1894

Archaeopus †† Rathbun, 1908

A. mexicanus Schweitzer, Feldmann, González-Barba and Vega, 2002 [Campanian-Maastrichtian, Baja California Sur]

Costacopluma †† Collins and Morris, 1975

C. bishopi Vega and Feldmann, 1992 [Coniacian, Guerrero] (Fraaije *et al.*, 2006; Martínez-Díaz *et al.*, 2016; Vega *et al.*, 2016)

C. grayi Feldmann and Portell, 2007 [late Maastrichtian, Coahuila] (Martínez-Díaz *et al.*, 2016; Vega *et al.*, 2016)

C. mexicana Vega and Perrillat, 1989 [late Campanian to early Maastrichtian of San Luis Potosí, Coahuila and Nuevo León] (Vega *et al.*, 1995a; Martínez-Díaz *et al.*, 2016; Vega *et al.*, 2016) (Fig. 5.13F)

Superfamily CANCROIDEA † Latreille, 1802

Atelecyclidae † Ortmann, 1893

Levicyclus †† Schweitzer, Feldmann, Gonzáles-Barba and Vega, 2002

L. tepetate Schweitzer, Feldmann, González-Barba and Vega, 2002 [Eocene, Baja California Sur]

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Anatolikos † Schweitzer and Feldmann, 2000

A. undecimspinosus †† Schweitzer, Feldmann, González-Barba and Ćosović, 2006b [middle Eocene, Baja California Sur]

Romaleon † Gistel, 1848

R. antennarium † (Stimpson, 1873) [Pliocene, Baja California Sur]

Cheiragonidae † Ortmann, 1893

Karasawaia †† Vega, Nyborg, Coutiño and Hernández-Monzón, 2008

K. markgrafi (Lőrenthey, 1907 [German version 1907[1909], as *Plagiolophus markgrafi*) (type) [Ypresian, Chiapas] (Vega *et al.*, 2008) (Fig. 5.13G)

Montezumella †† Rathbun, 1930

M. tubulata Rathbun, 1930 [Eocene: Priabonian, Baja California Sur]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Carcineretidae †† Beurlen, 1930

Carcineretes †† Withers, 1922

C. planetarius Vega, Feldmann, Ocampo and Pope, 1997 [early Maastrichtian, Chiapas] (Vega *et al.*, 2001b) (Fig. 5.13I)

Carcinidae † MacLeay, 1838

Xaiva † MacLeay, 1838

?*Xaiva* sp. [middle Eocene, Chiapas] (Vega *et al.*, 2008)

Icriocarcinidae Števčić, 2005

Icriocarcinus †† Bishop, 1988

I. xestos Bishop, 1988 [Maastrichtian, Baja California Sur] (Schweitzer *et al.*, 2002; Phillips *et al.*, 2014) (Fig. 5.13H)

Branchiocarcinus †† Vega, Feldmann and Sour-Tovar, 1995a

B. cornatus Feldmann and Vega, 1995 in Vega *et al.*, 1995a [Maastrichtian, San Luis Potosí] (Phillips *et al.*, 2014)

B. flectus (Rathbun, 1923a) [Maastrichtian, San Luis Potosí] (Phillips *et al.*, 2014; Vega *et al.*, 2016)

Longusorbiidae †† Karasawa, Schweitzer and Feldmann, 2008

Longusorbis †† Richards, 1975

L. quadratus Fraaije, Vega, van Bakel and Garibay-Romero, 2006 [Cenomanian-Coniacian, Guerrero]

L. eutychius Schweitzer, Feldmann and Karasawa, 2007c [Bartonian, Baja California Sur]

Macropipidae † Stephenson and Campbell, 1960

Maeandricampus †† Schweitzer and Feldmann, 2002

M. americanus (Rathbun, 1930) [Eocene, Baja California Sur]

Ophthalmoplax †† Rathbun, 1935b

O. brasiliana (Maury, 1930) (=*Mascaranada difuntaensis* Vega and Feldmann, 1991) [early to late Maastrichtian, Coahuila and Nuevo León] (Vega *et al.*, 2013; Vega *et al.*, 2016) (Fig. 5.13J)

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. nodosus Schweitzer, Feldmann, González-Barba and Vega, 2002 [Oligocene, Baja California Sur]

N. tajinensis Vega *et al.*, 1999 [middle Miocene, Veracruz]

Necronectes sp. [early Miocene, Chiapas] (Vega *et al.*, 2009)

Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. atecuicitlis †† Vega *et al.*, 1999 [early to middle Miocene, Chiapas and Veracruz] (Vega *et al.*, 2009)

Scylla † De Haan, 1833

S. costata †† Rathbun, 1919 [age and locality unknown] (Rathbun, 1930)

Podophthalminae † Dana, 1851c

Podophthalmus † Lamarck, 1801

?*Podophthalmus* sp. [late Cretaceous, Tamaulipas] (Rathbun, 1930)

Portunidae indet. [middle Eocene, Chiapas] (Vega *et al.*, 2008)

Portunidae indet. [middle Eocene, Baja California Sur] (Schweitzer *et al.*, 2006b)

Portunoidea indet. [early Miocene, Chiapas] (Vega *et al.*, 2009)

Superfamily CARPILIOIDEA † Ortmann, 1893

Palaeoxanthopsidae †† Schweitzer, 2003

Palaeoxanthopsis †† Beurlen, 1958b

P. meyapaquensis (Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001b, as *Paraxanthopsis meyapaquensis*) [early Maastrichtian, Chiapas]

Paraverrucoides †† Schweitzer, 2003

P. alabamensis (Rathbun, 1935b) [Paleocene (Selandian), Coahuila] (Vega *et al.*, 2007a; Martínez-Díaz *et al.*, 2017)

Verrucoides †† Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a

V. stenohedra Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a [early Eocene (Ypresian), Chiapas] (Vega *et al.*, 2008)

Tumidocarcinidae †† Schweitzer, 2005b

Lobonotus †† A. Milne-Edwards, 1863

L. mexicanus Rathbun, 1930 [Eocene, Baja California Sur] (Schweitzer *et al.*, 2002; Schweitzer *et al.*, 2006b; Schweitzer *et al.*, 2007a)

Zanthopsidae †† Vía Boada, 1959

Neozanthopsis †† Schweitzer, 2003

N. americanus (Rathbun, 1928) [?middle Eocene, Baja California Sur] (Vega *et al.*, 2006b)

Superfamily PILUMNOIDEA † Samouelle, 1819

Pilumnidae † Samouelle, 1819

Eumedoninae † Dana, 1853

Santeella †† Blow and Manning, 1996

S. lillyae Blow and Manning, 1996 [early Eocene (Ypresian), Chiapas] (Vega *et al.*, 2008)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurytium † Stimpson, 1862

Eurytium sp. [early Miocene, Chiapas; Pliocene, Veracruz] (Vega *et al.*, 2009)

Panopeus † H. Milne Edwards, 1834

P. veintensis †† Vega, Nyborg, Coutiño and Hernández-Monzón, 2008 [early Eocene (Ypresian), Chiapas]

Trapeziidae † Miers, 1886

Archaeotetra †† Schweitzer, 2005a

A. inornata Schweitzer, 2005a [middle Eocene, Baja California Sur]

Xanthidae † MacLeay, 1838

Xanthidae *incertae sedis*

?*Haydnella* †† Müller, 1984

?*Haydnella* sp. cf. *H. steiningeri* Müller, 1984 [early Miocene, Chiapas] (Vega *et al.*, 2009)

Megaxantho †† Vega, Feldmann, Garcia-Barrera, Filkorn, Pimentel and Avendaño, 2001b

M. zoque Vega, Feldmann, Garcia-Barrera, Filkorn, Pimentel and Avendaño, 2001b

[Maastrichtian, Chiapas] (Dietl and Vega, 2008)

Xanthoidea indet. [middle Eocene, Baja California Sur] (Schweitzer *et al.*, 2006b)

Clade THORACOTREMATA † Guinot, 1977

?Superfamily PINNOTHEROIDEA † De Haan, 1833

?Pinnotheridae † De Haan, 1833

?Pinnotherinae † De Haan, 1833

Viapinnixa †† Schweitzer and Feldmann, 2001

V. alvarezi Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a [Ypresian, Chiapas] (see also Vega *et al.*, 2008; Armstrong *et al.*, 2009)

V. perrilliatae Vega, Nyborg, Fraaye and Espinosa, 2007a [Paleocene (Selandian), Coahuila] (Armstrong *et al.*, 2009) (Fig. 5.13K)

Superfamily GRAPSOIDEA † MacLeay, 1838

Sesarmidae † Dana, 1851a

Sesarmidae indet. [Miocene (Aquitanian), Chiapas] (Serrano-Sánchez *et al.*, 2016)

Brachyura *incertae sedis*

?*Xanthosia zoquiapensis* Fraaije, Vega, van Bakel and Garibay-Romero, 2006 [Campanian, Guerrero]

Roemerus †† Bishop, 1983b

R. robustus Bishop, 1983b [Albian, Chiapas] (Vega *et al.*, 2006a)

5.4.6. Central and southern Florida, USA

Infraorder ANOMURA † MacLeay, 1838

Superfamily GALATHEOIDEA † Samouelle, 1819

Porcellanidae † Haworth, 1825

Petrolisthes † Stimpson, 1858

P. myakkensis †† Bishop and Portell, 1989 [late Pliocene, Charlotte County] (Fig. 5.14A)

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Coenobita † Latreille, 1829

Coenobitid indet. (crab habitational traces in neritid snail) [early Pleistocene, Hendy County] (Vermeij and Portell, 2013)

Petrochirus † Stimpson, 1858

P. bouvieri †† Rathbun, 1918 [1919] [early Pleistocene, Glades County] (Rathbun, 1935b)

P. diogenes † (Linnaeus, 1758) [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Ranininae † De Haan, 1839

Lophoranina †† Fabiani, 1910

Lophoranina sp. cf. *L. georgiana* †† (Rathbun, 1935b) [late Eocene of Alachua, Marion, and Lafayette Counties] (Portell, 2004) (Fig. 5.14B–C)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

Hepatus sp. [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. ocalana †† (Ross, Lewis and Scolaro, 1964) (as *Aparnocondylus*) [late Eocene of Alachua, Marion, and Lafayette Counties] (Portell, 2004)

C. robertsi †† Ross, Lewis and Scolaro, 1964 [late Eocene of Alachua, Marion, and Lafayette Counties] (Portell, 2004)

Calappa spp. [Plio-Pleistocene, central and southern peninsular Florida] (Portell and Agnew, 2004)

Calappilia †† A. Milne-Edwards, 1873

C. brooksi †† Ross and Scolaro, 1964 [late Eocene of Alachua, Marion, and Lafayette Counties] (Portell, 2004) (Fig. 5.14D–E)

C. calculosa †† Rumsey, Klompmaker and Portell, 2016 [late Eocene-early Oligocene, Suwannee County]

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

P. mediterranea † (Herbst, 1794) [early-middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004) (Fig. 5.14F)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Platylambrus † Stimpson, 1871

P. charlottensis †† (Rathbun, 1935b) [early Pleistocene, Charlotte County] (Fig. 5.14G–H)

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Pisinae † Dana, 1851d

Libinia † Leach, 1815

Libinia sp. [early-middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Mithracidae † MacLeay, 1838

Damithrax † Windsor and Felder, 2014

Damithrax sp. cf. *D. pleuracanthus* † (Stimpson, 1871) [late Pliocene to early Pleistocene, Sarasota County] (Klompmaker *et al.*, 2015a) (Fig. 5.14I)

Stenocionops † Desmarest, 1823

S. suwanneeana †† Rathbun, 1935b [late Eocene, Suwannee County]

Superfamily CANCROIDEA † Latreille, 1802

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Cancer † Latreille, 1802

C. irroratus † Say, 1817 [late Pleistocene-Holocene, Miami-Dade County] (Rathbun, 1935b)

Cheiragonidae † Ortmann, 1893

Montezumella †† Rathbun, 1930

M. microporosa †† Portell and Collins, 2002 [late Eocene, Alachua County] (Fig. 5.15F)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Ovalipidae † Spiridonov *et al.*, 2014

Ovalipes † Rathbun, 1898

O. stephensoni Williams, 1976 [early-middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Portunidae † Rafinesque, 1815

Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. depressifrons (Stimpson, 1859) [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

P. gibbesii (Stimpson, 1859) [early-middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

P. spinimanus Latreille, 1819 [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

?*Portunus* sp. [generic identification highly doubtful) [middle Eocene, Citrus County] (Ivany *et al.*, 1990; Portell, 2004)

Superfamily CARPILIOIDEA † Ortmann, 1893

Carpiliidae † Ortmann, 1893

Ocalina †† Rathbun, 1929

O. floridana Rathbun, 1929 (type) [late Eocene of Alachua, Levy, and Marion Counties] (Rathbun, 1935b) (Fig. 5.15A–C)

Palaeocarpilius †† A. Milne-Edwards, 1862

P. brodkorbi Lewis and Ross, 1965 [late Eocene, Alachua County] (Fig. 5.15D–E)

Superfamily ERIPHIOIDEA † MacLeay, 1838

Menippidae † Ortmann, 1893

Menippe † De Hann, 1833

M. mercenaria † (Say, 1818) [late Pleistocene, Pinellas County] (Portell and Schindler, 1991) (Fig. 5.15G–H)

M. nodifrons † Stimpson, 1859 [early Pleistocene, Glades County] (Rathbun, 1935b; Portell, 2004)

Superfamily † PILUMNOIDEA Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

Pilumnus † Leach, 1816

Pilumnus sp. [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Clade THORACOTREMATA † Guinot, 1977

Superfamily OCYPODOIDEA † Rafinesque, 1815

Ocypodidae † Rafinesque, 1815

Ocypode † Weber, 1795

O. quadrata † (Fabricius, 1787) [late Pleistocene-Holocene, Brevard County] (Rathbun, 1935b; Portell *et al.*, 2003)

Uca † Leach, 1814

Uca sp. [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

Superfamily PINNOTHEROIDEA † De Haan, 1833

Pinnotheridae † De Haan, 1833

Pinnothereliinae † Alcock, 1900b

Pinnixa † White, 1846

Pinnixa sp. [middle Pleistocene, Okeechobee County] (Agnew, 2001; Portell and Agnew, 2004)

5.5. Caribbean Islands & Bermuda

5.5.1. Anguilla

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. earlei †† Withers, 1924a [early Miocene, Cartouche Bay] (reported in Withers, 1924a as late Oligocene; see also Collins *et al*. 2009c)

Calappa sp. (claw only) [early Miocene, Cathedral Cave] (in Collins *et al.*, 2009c)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Parthenope † Weber, 1795

Parthenope sp. (claw fragment) [early Miocene, Cartouche Bay] (as late Oligocene in Withers, 1924a; see also Collins *et al.*, 2009c)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Scylla † De Haan, 1833

S. costata †† Rathbun, 1919 (claws only) [early Miocene, West side of Road Bay] (as late Oligocene in Withers, 1924a)

Podophthalminae † Dana, 1851c

Psygmophthalmus †† Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c

P. bifurcatus Collins *in* Collins *et al.*, 2009c [early Miocene, Betty Hill Quarry]

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Panopeus † H. Milne Edwards, 1834

Panopeus sp. (claw fragment) [early Miocene, Cartouche Bay] (reported in Withers, 1924a as late Oligocene; see also Collins *et al*. 2009c)

Brachyura *incertae sedis*

Brachyuran indet. ('*Lyreidus fastigatus'*, claw fragment) [Miocene, Crocus Bay] (Feldmann, 1992) **|Note 1|**

Note

|Note 1| A partial crab merus from Anguilla, initially described as representing the raninoid *Lyreidus fastigatus* Rathbun, 1919, was later removed from the genus by Feldmann (1992) based on the dissimilar nature of the merus to *Lyreidus*. Due to the poor and fragmentary nature of the material, it cannot be assigned to a particular group with certainty, thus we consider it here as 'Brachyura *incertae sedis*'.

5.5.2. Antigua

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Coenobita † Latreille, 1829

Coenobita sp. cf. *C. clypeatus* (Fabricius, 1787) [late Holocene, Burma Quarry] (Luque, 2017) |**Note1**|

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Mursia † Leach *in* Desmarest, 1823

M. granulosa †† Collins and Donovan, 2002 [late Oligocene, locality unknown] (see in Collins and Donovan, 2002, p. 145)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. summus Collins and Donovan, 1995 [late Oligocene, Nonsuch Bay] (Fig. 5. 16A)

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

Cardisoma sp. cf. *C. guanhumi* Latreille, 1828 [late Holocene, Burma Quarry] (Luque, 2017) |**Note 1**|

Gecarcinus † Leach, 1814 [in Leach, 1813–1815]

Gecarcinus sp. aff. *G. lateralis* (Freminville, 1835) [late Holocene, Burma Quarry] (Luque, 2017) **Note 1**|

Note

|Note 1| To date, these represent the first records of fossil anomurans and thoracotreme brachyurans from the island, and they are among the only fossil remains of *Coenobita*, *Gecarcinus*, and *Cardisoma* worldwide (Luque, 2017).

5.5.3. Aruba

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Mursia † Leach *in* Desmarest, 1823

M. creutzbergi †† Collins and Donovan, 2004 [Miocene-Pliocene, Rooi Taki]

5.5.4. Bahamas

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Gecarcinus † Leach, 1814 [in Leach, 1813–1815]

Gecarcinus sp. [late Holocene, San Salvador] (Locatelli, 2013)

5.5.5. Barbados

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CARPILIOIDEA † Ortmann, 1893

Carpiliidae † Ortmann, 1893

Carpilius † Desmarest, 1823

C. corallinus † (Herbst, 1783) [middle to late Pleistocene, Coral Rock] (in Collins *et al.*, 2009c)

Superfamily GONEPLACOIDEA † MacLeay, 1838

Chasmocarcinidae † Serène, 1964

Chasmocarcininae † Serène, 1964

Falconoplax †† Van Straelen, 1933a

F. bicarinella Collins and Morris, 1976 [early-middle Eocene Scotland Beds, Spa]

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. perornata Collins and Morris, 1976 (type) [early-middle Eocene Scotland Beds, Spa]

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Pisinae † Dana, 1851d

Herbstia † H. Milne Edwards, 1834

H. exserta †† Collins and Morris, 1976 [middle to late Pleistocene, Coral Rock]

Mithracidae † MacLeay, 1838

Maguimithrax † Klompmaker *et al.*, 2015a

M. spinosissimus † (Lamarck, 1818) [middle to late Pleistocene, Highgate] (in Collins and Morris, 1976)

Mithrax † Desmarest, 1823

M. hemphilli † Rathbun, 1892 [middle to late Pleistocene, Highgate] (in Collins and Morris, 1976)

M. hispidus † (Herbst, 1790) [= *M. caribbaeus* † Rathbun, 1920a] [middle to late Pleistocene, Gibbons] (in Collins and Morris, 1976)

M. aculeatus † (Herbst, 1790) (as *M. verrucosus* in H. Milne Edwards, 1832) [middle to late Pleistocene of Gibbons, Clapham and Garrison] (in Collins and Morris, 1976)

Teleophrys † Stimpson, 1860

T. ruber † (Stimpson, 1871, as *Mithraculus ruber*) [middle to late Pleistocene, Gibbons] (in Collins and Morris, 1976)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Atoportuninae † Števčić, 2005

Laleonectes † Manning and Chace, 1990

L. vocans † (A. Milne-Edwards, 1878) [middle to late Pleistocene, Coral Rock]

Portuninae † Rafinesque, 1815

Achelous † De Haan, 1833

A. gibbesii † (Stimpson, 1862) [middle to late Pleistocene, Coral Rock]

Superfamily PILUMNOIDEA † Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

*Pilum*nus † Leach, 1816

Pilumnus sp. (claw fragment) [Pleistocene, Clapham] (in Collins and Morris, 1976)

Superfamily XANTHOIDEA † MacLeay, 1838

Xanthidae † MacLeay, 1838

Actaeinae † Alcock, 1898

Paractaea † Guinot, 1969

P. nodosa † (Stimpson, 1860) [Pleistocene, Coral Rock] (as *Actaea rufopunctata* in Collins and Morris, 1976)

5.5.6. Bermuda

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

Cardisoma sp. cf. *C. guanhumi* † Latreille, 1828 [late Pleistocene, Crystal Cave] (Luque, 2017) |**Note 1**|

Gecarcinus † Leach, 1814 [in Leach, 1813–1815]

Gecarcinus sp. [late Pleistocene, Admiral Cave] (Luque, 2017; FLMNH online database |**Note 1**|

Note

|Note 1| To our knowledge, these represent the first records of fossil decapods from Bermuda (Luque, 2017). The generic affinities of the several hundreds of Bermudan '*Gecarcinus*' sp. fossil remains in the FLMNH Invertebrate Paleontology Collections are still to be confirmed, especially due to the potential occurrence of other non-congeneric terrestrial and semi-terrestrial crabs (Luque and Portell, personal observation).

5.5.7. Bonaire

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Calappilia †† A. Milne-Edwards, 1873

C. bonairensis Van Straelen, 1933b [middle to late Eocene (Lutetian-Priabonian), Southwest of Seroe Montagne]

Superfamily CANCROIDEA † Latreille, 1802

Cheiragonidae † Ortmann, 1893

Montezumella †† Rathbun, 1930

M. rutteni Van Straelen, 1933b [middle to late Eocene (Lutetian-Priabonian), Southwest of Seroe Montagne] (also reported in Collins and Donovan, 2005)

Superfamily CARPILIOIDEA † Ortmann, 1893

Carpiliidae † Ortmann, 1893

Ocalina †† Rathbun, 1929

O. sublevis Collins and Donovan, 2005 [middle to late Eocene (Lutetian-Priabonian), Southwest of Seroe Montagne]

5.5.8. Cuba

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Paguridae † Latreille, 1802

Paguridae indet. [late Pleistocene, US Guantanamo Bay Naval Station] (Collins *et al.*, 2009c).

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Ranininae † De Haan, 1839

Vegaranina †† van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

V. precocia (Feldmann, Vega, Tucker, García-Barrera and Avendaño 1996, as *Lophoranina precocious*) (type) [Maastrichtian, Cienfuegos Province] (in Varela and Rojas-Consuegra, 2009)

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

Raninoides sp. [early Miocene, Matanzas Province] (in Varela and Rojas-Consuegra, 2011c)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

Hepatus sp. [early Miocene, Matanzas Province] (in Varela and Rojas-Consuegra, 2011c)
Eriosachila †† Blow and Manning, 1996

E. cubaensis Varela and Rojas-Consuegra, 2011b [early Miocene, Matanzas Province]

Calappidae † De Haan, 1833

Calappidae indet. [late Pleistocene, US Guantanamo Bay Naval Station] (Collins *et al.*, 2009c).

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

Persephona sp. (merus fragment) [early Miocene, Sancti Spíritus Province] (in Varela and Rojas-Consuegra, 2009)

Iliacantha † Stimpson, 1871

Iliacantha sp. cf. *I. liodactylus* Rathbun, 1898 [early Miocene, Matanzas Province] (in Varela and Rojas-Consuegra, 2011c)

Superfamily ERIPHIOIDEA † MacLeay, 1838

Eriphiidae † MacLeay, 1838

Eriphia † Latreille, 1817

Eriphia sp. [early Miocene, Sancti Spíritus Province] (Varela, 2013)

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Pisinae † Dana, 1851d

Libinia † Leach, 1815

Libinia sp. [?Oligo–Miocene, locality unknown] (Varela, 2013)

Mithracidae † MacLeay, 1838

Mithrax † Desmarest, 1823

M. hispidus † (Herbst, 1790) [as *M. caribbaeus* in Rathbun, 1920a) [Pliocene–Pleistocene, La Habana] (see also Peñalver *et al.*, 1997)

?*Mithrax* sp. [late Pliocene, Matanzas Province and Sancti Spíritus Provinces] (Varela and Rojas-Consuegra, 2009; Varela, 2013)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Spinolambrus † Tan and Ng, 2007

S. lazaroi †† Varela, 2013 [early Miocene, Matanzas Province]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. collinsi Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c [early Miocene, Matanzas Province] (in Varela and Rojas-Consuegra, 2011c)

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. domingensis †† (Rathbun, 1919) [early Miocene, Matanzas Province] (Schweitzer *et al.*, 2006c; Varela and Rojas-Consuegra, 2011a)

Paraeuphylax †† Varela and Schweitzer, 2011

P. cubaensis (type) Varela and Schweitzer, 2011 [early Miocene, Matanzas Province]

Portuninae † Rafinesque, 1815

Arenaeus † Dana, 1851c

Arenaeus sp. [early Miocene, Sancti Spíritus Province] (Varela, 2013)

Callinectes † Stimpson, 1862

Callinectes sp. [early Miocene, Sancti Spíritus Province] (Varela, 2013)

Portunus † Weber, 1795

P. oblongus †† Rathbun, 1920b [early Miocene, Matanzas Province] (in Varela and Rojas-Consuegra, 2009)

Portunus sp. (claw fragments) [early Miocene, Sancti Spíritus Province] (in Schweitzer *et al.*, 2006c and Varela and Rojas-Consuegra, 2011a)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurytium † Stimpson, 1859

Eurytium sp. [early Miocene, Sancti Spíritus Province] (Varela, 2013)

Panopeus † H. Milne Edwards, 1834

Panopeus sp. [early Miocene, Sancti Spíritus Province] (in Varela and Rojas-Consuegra, 2009; Varela and Rojas-Consuegra, 2011a)

Panopeidae indet. [late Pleistocene, US Guantanamo Bay Naval Station] (Collins *et al*. 2009c)

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Gecarcinus † Leach, 1814 [in Leach, 1813–1815]

G. ruricola † (Linnaeus, 1758) [late Pleistocene, Matanzas Province] (identified by Mary J. Rathbun in Richards, 1935)

5.5.9. Curaçao

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Notopodinae † Serène and Umali, 1972

Ranilia † H. Milne Edwards, 1837

R. constricta † (A. Milne-Edwards, 1880a) [Pliocene, Salina Sint Michiel] (Stepp, 2014) (Fig. 5.16B)

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

R. lamarcki † A. Milne-Edwards and Bouvier, 1923 [Pliocene, Salina Sint Michiel] (Stepp, 2014)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. lineatinus †† Collins and Todd *in* Todd and Collins, 2005 [Pliocene, Salina Sint Michiel] (Stepp, 2014)

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. galloides † Stimpson, 1859 [Pliocene, Salina Sint Michiel] (Stepp, 2014)

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Myropsis † Stimpson, 1871

M. quinquespinosa † Stimpson, 1871 [Pliocene, Salina Sint Michiel] (Stepp, 2014)

Superfamily MAJOIDEA † Samouelle, 1819

Mithracidae † MacLeay, 1838

Maguimithrax † Klompmaker *et al.*, 2015a

M. spinosissimus † (Lamarck, 1818) [Pliocene, Salina Sint Michael] (Stepp, 2014; Klompmaker *et al.*, 2015a)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Portuninae † Rafinesque, 1815

Achelous † De Haan, 1833

A. sebae † (H. Milne Edwards, 1834) [Pliocene, Salina Sint Michiel] (Stepp, 2014)

5.5.10. Dominican Republic

Infraorder ANOMURA † MacLeay, 1838

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Dardanus † Paul'son, 1875

D. squamatus †† Collins *in* Collins *et al.*, 2009c [late Miocene–early Pliocene, Río Gurabo and Río Mao]

Petrochirus † Stimpson, 1858

P. inequalis †† Rathbun, 1919 [Pleistocene, Rio Gurabo and Santo Domingo] (Collins *et al.*, 2009c)

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. guraboensis †† Collins *in* Collins *et al.*, 2009c [late Miocene, Rio Gurabo, Rio Cana and Rio Mao]

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. flammea † (Herbst, 1794 [in 1782–1804]) [late Miocene, Rio Gurabo and Santo Domingo] (Collins *et al.*, 2009c)

Calappa sp. [late Miocene–early Pliocene, Rio Gurabo] (Collins *et al.*, 2009c)

Cryptosoma † Brullé, 1839

C. bairdii † (Stimpson, 1862) [late Miocene, Rio Gurabo] (Collins *et al.*, 2009c)

Superfamily CARPILIOIDEA † Ortmann, 1893

Tumidocarcinidae †† Schweitzer, 2005b

Lobonotus †† A. Milne-Edwards, 1863

L. sculptus A. Milne-Edwards, 1863 (=*Archaeopilumnus caelatus* Rathbun, 1919) [late Miocene, Rio Gurabo] (Rathbun, 1919, 1920b; Collins *et al.*, 2009c; Ossó *et al.*, 2014)

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

P. prepunctata †† Rathbun, 1919 [late Miocene, Rio Gurabo and Rio Mao]

Iliacantha † Stimpson, 1871

Iliacantha sp. [early Miocene, Rio Gurabo] (in Collins *et al.*, 2009c)

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Mesorhoea † Stimpson, 1871

M. mauryae †† Rathbun, 1919 [late Miocene–early Pliocene, Río Cana and Santo Domingo] (Collins *et al.*, 2009c)

Platylambrus † Stimpson, 1871

P. obscura †† Rathbun, 1919 [Miocene, Santo Domingo]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Scylla † De Haan, 1833

S. costata †† Rathbun, 1919 [Miocene, valley of Yaque del Norte River] |**Note 1**|

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. domingensis †† (Rathbun, 1919, as *Podophthalmus domingensis*) [Miocene, valley of Yaque del Norte River] |**Note 1**|

Psygmophthalmus †† Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c

P. bifurcatus Collins *in* Collins *et al.*, 2009c [age uncertain, Rio Cana]

Sandomingia †† Rathbun, 1919

S. yaquiensis Rathbun, 1919 [late Miocene–early Pliocene, Río Cana and Rio Yaque del Norte] (Collins *et al.*, 2009c) |**Note 1**|

Portuninae † Rafinesque, 1815

Callinectes † Stimpson, 1862

C. declivis †† Rathbun, 1918 [1919] (fingers only) [late Miocene, Rio Gurabo and Rio Mao Santo Domingo] (in Collins *et al.*, 2009c)

Portunus † Weber, 1795

P. gabbi †† Rathbun, 1919 [Miocene, valley of Yaque del Norte River] |**Note 1**|

P. oblongus †† Rathbun, 1920b [late Miocene–early Pliocene, Río Cana]

P. tenuis †† Rathbun, 1919 (type) (claws only) [Miocene of Yaque Valley, Santo Domingo]

Rathbunites †† Schweitzer, Dworschak and Martin, 2011 [=*Rathbunella* †† Collins *in* Collins *et al.*, 2009c]

R. pentaspinosa (Collins *in* Collins *et al.*, 2009c) (type) [late Miocene–early Pliocene, Río Cana]

Superfamily PILUMNOIDEA † Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

*Pilum*nus † Leach, 1816

P. subequus †† Rathbun, 1919 (claws only) [Miocene of Yaque Valley, Santo Domingo] |**Note 1**|

Pilumnus sp. [late Miocene, Rio Gurabo] (Collins *et al.*, 2009c)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurypanopeus † A. Milne-Edwards, 1880

Eurypanopeus sp. aff. *E. crenatus* H. Milne Edwards, 1834 [age uncertain, Rio Cana] (Collins *et al.*, 2009c)

Panopeus † H. Milne Edwards, 1834

Panopeus sp. [late Miocene, Rio Gurabo] (Collins *et al.*, 2009c)

Note

|**Note 1**| As previously noticed by Collins *et al*. (2009c, p. 62), Rathbun (1919) reported a handful of fossil crabs as coming from Haiti, but in fact come from lower Miocene rocks exposed along the "Lower half of the valley of the Yaqui[sic] del Norte River, in the northern part of Santo Domingo" in Dominican Republic, most remarkable being *Scylla costata, Portunus gabbi, Euphylax dominguensis* (as *Podophthalmus*), and *Sandomingia yaquiensis*.

5.5.11. The Grenadines

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Calappa † Weber, 1795

Calappa sp. cf. *C. springeri* (Rathbun, 1931) [middle Miocene, Carriacou] (Donovan *et al.*, 2003; Collins *et al.*, 2009c)

Superfamily ERIPHIOIDEA † MacLeay, 1838

Platyxanthidae † Guinot, 1977

Platyxanthus † A. Milne-Edwards, 1863

Platyxanthus sp. [middle Miocene, Carriacou] (Collins *et al.*, 2009c)

5.5.12. Haiti

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily MAJOIDEA † Samouelle, 1819

Mithracidae † MacLeay, 1838

Mithrax † Desmarest, 1823

?*Mithrax* sp. [Pleistocene, Môle St. Nicolas in Nord-West department] (Rathbun, 1923b) **|Note 1|**

Superfamily PARTHENOPOIDEA † MacLeay, 1838

?Parthenopoid indet. (claw fragment) [early Miocene, Centre department] **|Note 2|**

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. haitensis †† Rathbun, 1923b [early Miocene, Centre department] **|Note 1|**

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Panopeus † H. Milne Edwards, 1834

?*Panopeus* sp. indet. (fingers only) [early Miocene, Centre department] (Rathbun, 1923b) **|Note 2|**

Eubrachyuran indet. (claw) (as ?*Zanthopsis* indet. in Rathbun, 1923b) [Eocene, Artibonite department] **|Note 2|**

Notes

|Note 1| As previously noticed by Collins *et al.* (2009c, p. 62), a handful of fossil crabs reported by Rathbun (1919) as coming from Haiti are in fact from the Miocene of Dominican Republic.

|Note 2| Rathbun (1923b) assigned some fossil cheliped fragments from Haiti to *Parthenope*, *Panopeus*, and '*Zanthopsis*' with uncertainty. Indeed, the generic and familial placements need to be re-examined.

5.5.13. Jamaica

Infraorder ANOMURA † MacLeay, 1838

Superfamily GALATHEOIDEA † Samouelle, 1819

Porcellanidae † Haworth, 1825

Petrolisthes † Stimpson, 1858

Petrolisthes sp. [late Pleistocene, parish of St. Ann] (Morris, 1993)

Superfamily HIPPOIDEA † Latreille, 1825

Albuneidae † Stimpson, 1858

Albunea † Weber, 1795

Albunea sp. [late Pleistocene, parish of St. Ann) (Morris, 1993)

Superfamily PAGUROIDEA † Latreille, 1802

Diogenidae † Ortmann, 1892a

Dardanus † Paul'son, 1875

D. portmorantensis †† Collins and Donovan, 2012 [Pleistocene, parish of St. Thomas]

Petrochirus † Stimpson, 1858

P. bahamensis † (Herbst, 1791) [late Pliocene to late Pleistocene, parish of St. Thomas] (Collins and Portell, 1998; Collins *et al.*, 2009a; Collins and Donovan, 2012) (Fig. 5.16C)

Petrochirus sp. [late Pleistocene, parish of St. Ann] (Morris, 1993)

Paguristes † Dana, 1851a

Paguristes sp. cf. *P. lymanni* A. Milne-Edwards and Bouvier, 1893 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Paguristes sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Infraorder BRACHYURA † Latreille, 1802

Superfamily HOMOLODROMIOIDEA † Alcock, 1900a

Goniodromitidae †† Beurlen, 1932

Trechmannius †† Collins and Donovan, 2006

T. circularis Collins and Donovan, 2006 (type) [early Paleocene, Portland]

Superfamily DROMIOIDEA † De Haan, 1833

Dynomenidae † Ortmann, 1892a

Dynomene † Desmarest, 1823

D. variabilis †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Kromtitis †† Müller, 1984

K. spinulata Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Superfamily PALAEOCORYSTOIDEA †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Palaeocorystidae †† Lőrenthey *in* Lőrenthey and Beurlen, 1929

Cretacoranina †† Mertin, 1941

C. trechmanni (Withers, 1927, as *Ranina trechmanni*) [Maastrichtian, parish of St. James] (Morris, 1993)

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Raninoidinae † Lőrenthey *in* Lőrenthey and Beurlen, 1929

Raninoides † H. Milne Edwards, 1837

R. louisianensis † Rathbun, 1933 [Pleistocene, late Pleistocene, parish of St. Thomas] (Collins and Donovan, 1998)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. praecox †† Collins, Donovan and Dixon, 1997 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Hepatus sp. † [late Pliocene, parish of St, Thomas] (Collins and Portell, 1998)

Calappidae † De Haan, 1833

Calappa † Weber, 1795

Calappa sp. cf. *C. gallus* † (Herbst, 1803) [late Pleistocene, parish of St. Ann] (Morris, 1993)

C. springeri † Rathbun, 1931 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997) (Fig. 5.16D)

Calappa sp. aff. *C. springeri* † Rathbun, 1931 [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

Persephona punctata † (Linnaeus, 1758) [late Pleistocene, parish of St. Thomas) (Collins *et al.*, 1997)

Persephona sp. aff. *P. punctata* † (Linnaeus, 1758) [late Pliocene, parish of St. Ann) (Morris, 1993)

?*Persephona* sp. [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Uhlias † Stimpson, 1871

Uhlias cf. *U. limbatus* † Stimpson, 1871 [late Pleistocene, parish of St. Ann) (Morris, 1993)

Leucosiidae *incertae sedis*

Duncanitrix †† Schweitzer, Dworschak and Martin, 2011 [=*Duncania* Portell and Collins, 2004]

D. jamaicensis (Portell and Collins, 2004) [early Miocene, parish of Trelawny]

Superfamily PARTHENOPOIDEA † MacLeay, 1838

Parthenopidae † MacLeay, 1838

Parthenopinae † MacLeay, 1838

Mesorhoea † Stimpson, 1871

Mesorhoea sp. aff. *M. sexspinosa* † Stimpson, 1871 [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Platylambrus † Stimpson, 1871

Platylambrus sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily MAJOIDEA † Samouelle, 1819

Epialtidae † MacLeay, 1838

Pisinae † Dana, 1851d

Chlorilia † Dana, 1851d

Chlorilia sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Libinia † Leach, 1815

L. milnei (Collins and Donovan, 2012) [Pleistocene, parish of Portland]

Pitho † Bell, 1836

P. anisodon † (von Martens, 1872) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997)

Pitho sp. (claw dactylus) [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Rochinia † A. Milne-Edwards, 1875

Rochinia sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Mithracidae † MacLeay, 1838

Damithrax † Windsor and Felder, 2014

D. unguis †† (Portell and Collins, 2004) [early Miocene, parish of Trelawny] (see Klompmaker *et al.*, 2015a)

Maguimithrax † Klompmaker *et al.*, 2015a

M. spinosissimus † (Lamarck, 1818) [late Pleistocene, parish of St. Ann] (Morris, 1993)

Mithraculus † White, 1847

Mithraculus sp. aff. *M. coryphe* (Herbst, 1790) [late Miocene, parish of St. Thomas] (Collins *et al.*, 2010)

M. forceps † A. Milne-Edwards, 1875 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a) **|Note 1|**

Mithraculus sp. cf. *M. forceps* † A. Milne-Edwards, 1875 [late Pleistocene, parish of St. Ann] (Morris, 1993)

Mithrax † Desmarest, 1823

M. arawakum †† Klompmaker *et al.*, 2015a [early Miocene, parish of Trelawny]

Mithrax sp. cf. *M. hispidus* † (Herbst, 1790) [= *M. caribbaeus* † Rathbun, 1920a] [late Pleistocene, parish of St. Ann] (Morris, 1993)

M. aculeatus † (Herbst, 1782–1804) (= *M. verrucosus* † H. Milne Edwards, 1832) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Nemausa † A. Milne-Edwards, 1875

N. acuticornis † (Stimpson, 1871) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

N. donovani †† (Portell and Collins, 2004) [early Miocene, parish of Trelawny]

N. windsorae †† Klompmaker *et al.*, 2015a [early Miocene, parish of Trelawny]

Teleophrys † Stimpson, 1860

T. acornis †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Oregoniidae † Garth, 1958

Hyas † Leach, 1814 [in Leach, 1813–1815]

Hyas sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily CANCROIDEA † Latreille, 1802

Cancridae † Latreille, 1802

Cancrinae † Latreille, 1802

Cancer † Linnaeus, 1758

Cancer sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Carcineretidae †† Beurlen, 1930

Carcineretes †† Withers, 1922

C. woolacotti Withers, 1922 [Maastrichtian, parishes of Clarendon and St. James]

Ovalipidae † Spiridonov *et al.*, 2014

Ovalipes † Rathbun, 1898

Ovalipes sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Portunidae † Rafinesque, 1815

Atoportuninae † Števčić, 2005

Laleonectes † Manning and Chace, 1990

L. vocans † (A. Milne-Edwards, 1878) [late Pleistocene, parish of St. Thomas]

Podophthalminae † Dana, 1851c

Euphylax † Stimpson, 1862

E. fortispinosus †† Collins, Donovan, Lindsay and Simpson, 2001 [early Pleistocene, parish of St. Thomas] (Collins e*t al.* 2009c)

Portuninae † Rafinesque, 1815

Achelous † De Haan, 1833

A. sebae † (H. Milne Edwards, 1834) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Callinectes † Stimpson, 1862

C. jamaicensis †† Withers, 1924b (claw fragment only) [middle Eocene (Lutetian), parish of Hanover] (Morris, 1993)

Callinectes sp. aff. *C. sapidus* † Rathbun, 1896 [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Callinectes sp. cf. *C. toxodes* † Ordway, 1863 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997)

Portunus † Weber, 1795

Portunus sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Pseudoachelous †† Portell and Collins, 2004

P. schindleri Portell and Collins, 2004 (type) [early Miocene, parish of Trelawny]

Superfamily CARPILIOIDEA † Ortmann, 1893

Carpiliidae † Ortmann, 1893

Carpilius † Desmarest, 1823

C. corallinus † (Herbst, 1783) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Ocalina †† Rathbun, 1929

O. haldixoni Collins and Donovan, 2006 [middle to late Eocene, parish of Portland]

Palaeoxanthopsidae †† Schweitzer, 2003

Palaeoxanthopsis †† Beurlen, 1958b

Palaeeoxanthopsis sp. (as ?*Paranecrocarcinus* sp. in Morris, 1993, fig. 1.6) [?Maastrichian, unknown] |**Note 2**|

?Palaeoxanthopsidae *incertae sedis* (as *Necrocarcinus* sp. in Morris, 1993) [?Maastrichian, unknown] |**Note 2**|

Superfamily DAIROIDEA † Serène, 1965

Dairidae † Serène, 1965

Daira † De Haan, 1833

D. vulgaris †† Portell and Collins, 2004 [early Miocene, parish of Trelawny] (Fig. 5.16E)

Superfamily ERIPHIOIDEA † MacLeay, 1838

Eriphiidae † MacLeay, 1838

Eriphia † Latreille, 1817

E. gonagra xaymacaensis †† Collins and Donovan, 1998 (type) [late Pleistocene, parish of St. Thomas]

Eriphia sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily PILUMNOIDEA † Samouelle, 1819

Pilumnidae † Samouelle, 1819

Pilumninae † Samouelle, 1819

Pilumnus † Leach, 1816

Pilumnus sp. aff. *P. pannosus* † Rathbun, 1898 [late Pliocene, parish of St. Thomas]

Pilumnus sp. aff. *P. sayi* † Rathbun, 1897b [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997)

Pilumnus sp. aff. *P. spinossimus* † Rathbun, 1898 [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurypanopeus † A. Milne-Edwards, 1880

E. abbreviatus † (Stimpson, 1860) [late Pleistocene, parish of St. Ann] (Morris, 1993)

Eurypanopeus sp. cf. *E. depressus* † (Smith, 1869a) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997; Collins and Donovan, 2012)

Eurypanopeus sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Eurytium † Stimpson, 1859

Eurytium sp. cf. *E. limosum* † (Say, 1818) [late Pliocene to late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997; Collins and Portell, 1998; Collins *et al.*, 2009c)

Hexapanopeus † Rathbun, 1898

H. caribbaeus † (Stimpson, 1871) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 1997)

Lophopanopeus † Rathbun, 1898

L. corallinus †† Portell and Collins, 2004 [early Miocene, parish of Trelawny] (Fig. 5.16F)

L. toomeyorum †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Neopanope † A. Milne-Edwards, 1880

Neopanope sp. [late Pliocene, parish of St. Thomas] (Collins and Portell, 1998)

Panopeus † H. Milne Edwards, 1834

P. herbstii † H. Milne Edwards, 1834 (claw only) [late Pliocene-late Pleistocene, parishes of St. Thomas and St. Ann] (Morris, 1993; Collins and Portell, 1998)

P. nanus †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

P. rugosus † A. Milne-Edwards, 1880b (claw only) [late Pleistocene, parish of St. Thomas] (Collins and Donovan, 2012)

Pseudorhombilidae † Alcock, 1900b

Nanoplax † Guinot, 1967

N. xanthiformis † (A. Milne-Edwards, 1880b) [late Pleistocene, parish of St. Thomas] (Collins and Portell, 1998)

Trapeziidae † Miers, 1886

Trapezia † Latreille, 1828

T. prisca †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Xanthidae † MacLeay, 1838

Actaeinae † Alcock, 1898

Actaea † De Haan, 1833

A. acantha † (H. Milne Edwards, 1834) [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

A. bifrons † Rathbun, 1898 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Actaeops †† Portell and Collins, 2004

A. frontalis Portell and Collins, 2004 (type) [early Miocene, parish of Trelawny]

Chlorodiellinae † Ng and Holthuis, 2007

Chlorodiella † Rathbun, 1897a (= *Chlorodius* H. Milne Edwards, 1834)

C. occidentalis †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Xanthinae † MacLeay, 1838

Leptodius † A. Milne-Edwards, 1863

L. granulatus †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Micropanope † Stimpson, 1871

?*M. nuttingi* † (Rathbun, 1898) [late Pleistocene, parish of St. Thomas] (Collins and Portell, 1998)

Micropanope sp. cf. *M. polita* Rathbun, 1893 [late Pleistocene, parish of St. Ann] (Morris, 1993; Collins *et al.*, 2001)

Micropanope sp. cf. *M. spinipes* A. Milne-Edwards, 1880 [late Pliocene to late Pleistocene, parishes St, Thomas and St. Ann] (Morris, 1993; Collins and Portell, 1998)

M. pulcherrima †† Portell and Collins, 2004 [early Miocene, parish of Trelawny]

Micropanome sp. aff. *M. truncatifrons* † Rathbun, 1898 [late Pleistocene, parish of St. Thomas] (Collins *et al.*, 2009a)

Cycludius † Dana, 1851 (= *Phymodius* A. Milne-Edwards, 1863)

Cycludius sp. cf. *C. maculatus* (Stimpson, 1860) [late Pleistocene, parish of St. Ann] (Morris, 1993)

Xanthoidea *incertae sedis*

?*Xanthilites rathbunae* †† Withers, 1924b [middle Eocene (Lutetian), parish of Hanover] (Morris, 1993)

Clade THORACOTREMATA † Guinot, 1977

Superfamily GRAPSOIDEA † MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

C. guanhumi † Latreille, 1828 [late Pleistocene, parish of St. Thomas] (Collins and Donovan, 1998, 2012)

Grapsidae MacLeay, 1838

Pachygrapsus † Randall, 1840

Pachygrapsus sp. [late Pleistocene, parish of St. Ann] (Morris, 1993)

Sesarmidae † Dana, 1851a

Sesarma † Say, 1817

Sesarma sp. cf. *cookei* Hartnoll, 1971a (as S. *primigenium* in Collins, Mitchell and Donovan, 2009b) [late Pleistocene, parish of St. Elizabeth] (Donovan and Dixon, 1998; Baalbergen and Donovan, 2013; Donovan, 2016) |**Note 3**|

Varunidae H. Milne Edwards, 1853

?*Varuna* H. Milne Edwards, 1830

?*Varuna* sp. [middle Eocene, parish of St. James] (Morris, 1993)

Superfamily OCYPODOIDEA † Rafinesque, 1815

Ocypodidae † Rafinesque, 1815

Uca † Leach, 1814

Uca sp. [late Pleistocene, parish of St. Ann] (Morris, 1993)

Notes

|Note 1| Collins *et al.* (2009a) listed this taxon from the late Pliocene Bowden Formation in error.

|Note 2| Two fragmentary dorsal carapaces from the Late Cretaceous (stage unknown) were assigned by Morris (1993) to the necrocarcinoids *Necrocarcinus* and ?*Paranecrocarcinus* (Morris, 1993, fig. 1.5 and 1.6, respectively), but both Jamaican specimens lack diagnostic features of the families Necrocarcinidae and Paranecrocarcinidae. The overall configuration of the carapace regions and grooves, the absence of longitudinal rows of tubercles axially and along the branchial regions, the lack of coarse granulations, and the absence of postrostral slits, preclude placement among *Necrocarcinus*, ?*Paranecrocarcinus*, or any genus or family of Necrocarcinoidea (Schweitzer *et al.*, 2016). The specimens seem to be better placed among the heterotremous Eubrachyura, particularly the family Palaeoxanthopsidae. The specimen referred to '?*Paranecrocarcinus*' seems to be congeneric with *Palaeoxanthopsis* Beurlen, 1958b, and shares some overall similarities with *P. tylotus* from the late Maastrichtian of Puerto Rico

(Schweitzer *et al.*, 2008). The specimen reported as '*Necrocarcinus*' also has an overall palaeoxanthopsid appearance, but its systematic affinities are yet to be determined.

|Note 3| Cheliped remains of *Sesarma* sp. cf. *S. cookei* from the late Pleistocene of Jamaica were initially identified as *Gecarcinus* cf. *ruricola* (Collins in Donovan and Dixon, 1998), later as belonging to *S. primigenium* (Collins *et al.,* 2009b), and more recently as *Sesarma* sp. cf. *S. cookei* (Baalbergen and Donovan, 2013; Donovan, 2016; Luque, 2017).

5.5.14. Puerto Rico

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Ranininae † De Haan, 1839

Vegaranina †† van Bakel, Guinot, Artal, Fraaije and Jagt, 2012a

V. precocia (Feldmann, Vega, Tucker, García-Barrera and Avendaño 1996, as *Lophoranina precocious*) [late Maastrichtian, Sabana Grande] (Schweitzer *et al.*, 2008)

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA † De Haan, 1833

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. pavimenta †† Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c [early Miocene, San Sebastián]

Superfamily CARPILIOIDEA † Ortmann, 1893

Palaeoxanthopsidae †† Schweitzer, 2003

Palaeoxanthopsis †† Beurlen, 1958b

P. tylotus Schweitzer, Velez-Juarbe, Martinez, Collmar Hull, Feldmann and Santos, 2008 [late Maastrichtian, Sabana Grande]

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. collinsi Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c [Oligocene-Miocene, San Sebastián and Yauco] (Schweitzer *et al.*, 2008) (Fig. 5.16G)

N. proavitus †† (Rathbun, 1918 [1919]) [Miocene, uncertain] (Gordon, 1966b; Schweitzer *et al.*, 2006c)

Scylla † De Haan, 1833

S. costata †† Rathbun, 1919 (Miocene, San Sebastián and Yauco] (Schweitzer *et al.*, 2008)

Podophthalminae † Dana, 1851c

Psygmophthalmus †† Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c

P. lares Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c (type) [early Miocene, San Sebastián]

Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. oblongus †† Rathbun, 1920b [Miocene, uncertain] (Gordon, 1966b; Schweitzer *et al.*, 2006c)

P. yaucoensis †† Schweitzer, Iturralde-Vinent, Hetler and Velez-Juarbe, 2006c [early Oligocene (Rupelian), Yauco]

Superfamily XANTHOIDEA † MacLeay, 1838

Panopeidae † Ortmann, 1893

Panopeinae † Ortmann, 1893

Eurytium † Stimpson, 1859

E. granulosum †† Schweitzer, Velez-Juarbe, Martinez, Hull, Feldmann and Santos, 2008 [Miocene, near Ponce] (Schweitzer *et al.*, 2008)

Clade THORACOTREMATA Guinot, 1977

Superfamily GRAPSOIDEA MacLeay, 1838

Gecarcinidae † MacLeay, 1838

Cardisoma † Latreille, 1828

C. guanhumi † Latreille, 1828 [Pleistocene, Utuado] (Schweitzer *et al.*, 2008)

5.5.15. Saint Barthélemy (St. Barts)

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA De Haan, 1833

Aethridae † Dana, 1851c

Eriosachila †† Blow and Manning, 1996

E. bartholomaensis (Rathbun, 1919, as *Zanthopsis bartholomaensis*) [Eocene, St. Bartholomew]

5.5.16. Saint Martin

Infraorder BRACHYURA † Latreille, 1802

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA De Haan, 1833

Calappidae † De Haan, 1833

Tutus †† Collins *in* Collins *et al.*, 2009c

T. granulosus Collins *in* Collins *et al.*, 2009c [Miocene of Leeward Islands, Tintamare Island]

5.5.17. Trinidad

Infraorder BRACHYURA † Latreille, 1802

Superfamily RANINOIDEA † De Haan, 1839

Raninidae † De Haan, 1839

Ranininae † De Haan, 1839

Lophoranina †† Fabiani, 1910

L. porifera (Woodward, 1866) [‘Tertiary’ indet, San Fernando]

Clade EUBRACHYURA † Saint Laurent, 1980

HETEROTREMATA † Guinot, 1977

Superfamily CALAPPOIDEA De Haan, 1833

Aethridae † Dana, 1851c

Hepatus † Latreille, 1802

H. nodosus †† Collins and Morris, 1976 [middle Miocene, Manzanilla Bay]

Calappidae † De Haan, 1833

Calappa † Weber, 1795

C. cuspidata †† (Guppy, 1909, as *Ranina cuspidata*) [Oligocene, Tamana District] (Pasini and Garassino, 2017)

Superfamily HEXAPODOIDEA † Miers, 1886

Hexapodidae † Miers, 1886

Palaeopinnixa †† Vía Boada, 1966

P. intermedia (Collins and Morris, 1976, as *Thaumastoplax intermedia*) [middle Miocene, Montserrat]

P. perornata Collins and Morris, 1976 (type) [Miocene, Montserrat]

Superfamily LEUCOSIOIDEA † Samouelle, 1819

Leucosiidae † Samouelle, 1819

Ebaliinae † Stimpson, 1871

Persephona † Leach, 1817

P. punctata † (Linnaeus, 1758) [Miocene-Pliocene, Manzanilla Bay] (Collins and Morris, 1976)

Superfamily PORTUNOIDEA † Rafinesque, 1815

Portunidae † Rafinesque, 1815

Necronectinae † Glaessner, 1928

Necronectes †† A. Milne-Edwards, 1881b

N. proavitus †† (Rathbun, 1918 [1919]) [middle Miocene, near Caparo Saca Manteca] (Collins and Morris, 1976)

Portuninae † Rafinesque, 1815

Portunus † Weber, 1795

P. oblongus †† Rathbun, 1920b [middle Miocene, Manzanilla Bay and Montserrat] (Collins and Morris, 1976)

5.6. Final Remarks

This revision of the anomuran and brachyuran fossil record in the tropical Americas demonstrates a diversity and abundance previously unassessed, with 32 superfamilies, 69 families, 190 genera, and 415 species properly recognized (Figs 5.1D, 5.17). Most superfamilies and families in this checklist have pantropical distributions, although there is a considerable degree of endemism at the generic and specific levels, particularly during the Early Cretaceous of Northern South America and Mexico, e.g., *Brazilomunida*, *Protaegla*, *Maurimia*, *Dynomenopsis*, *Araripecarcinus*, *Bellcarcinus*, *Colombicarcinus*, *Planocarcinus*, *Tepexicarcinus*, and several new Cretaceous and Paleogene families, genera and species under study. However, the sampling bias in the tropics is still high, with most fossil records known from Cenozoic deposits through the continental and insular Caribbean. This is exemplified by countries like Jamaica (with 32 fam., 65 gen., and 71 spp.) or Panama (with 24 fam., 41 gen., and 47 spp.), that independently account for more fossil occurrences than much larger countries like Bolivia, Colombia, Ecuador and Peru all combined (Figs 5.1D, 5.17).

Despite this, several recent findings – particularly from northern South America – represent the oldest members of their genera, families, superfamilies, or even new lineages, and suggest a more complex phylogenetic scenarios than currently depicted (Luque *et al*., 2016). Furthermore, several of these new findings challenge the paradigm of a high latitude origin for several groups, and extend their stratigraphic and paleogeographic ranges into the equatorial Neotropics, highlighting the role and importance of the tropical Americas in the origin and evolution of decapod crustaceans through time.

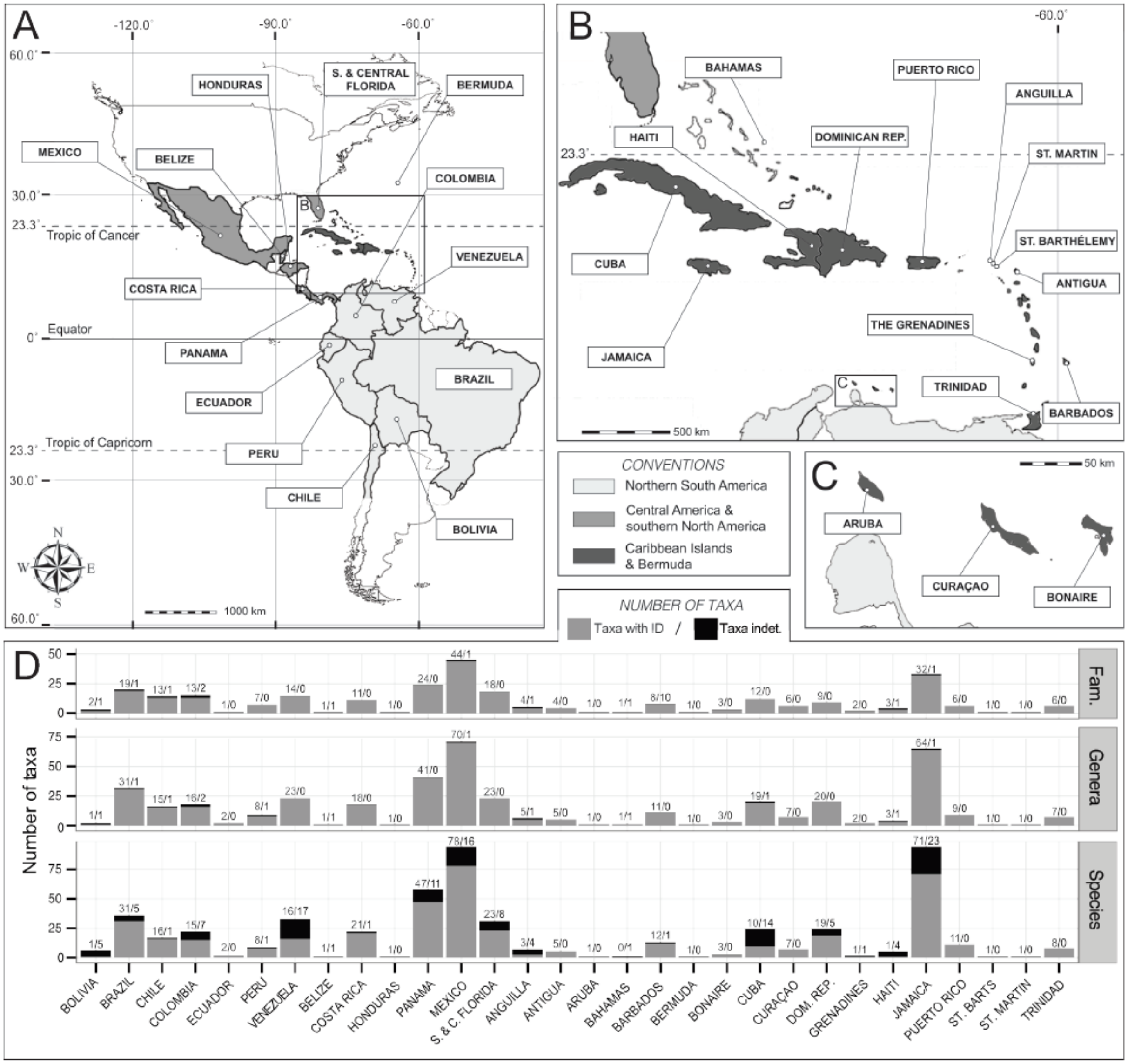


Figure 5.1. Location map of the tropical and subtropical American countries, states, territories, or islands where fossil anomurans and brachyurans have been discovered/reported to date. A, northern South America (light gray) with records from Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, and Venezuela; continental Central America and southern North America (intermediate gray), with records from Belize, Costa Rica, Honduras, Panama, Mexico, and southern and central Florida; B, Caribbean Islands and Bermuda (dark gray), with records from Anguilla, Antigua, Aruba, Bahamas, Barbados, Bermuda, Bonaire, Cuba, Curaçao, Dominican Republic, the Grenadines, Haiti, Jamaica, Puerto Rico, Saint Bartélemy, Saint Martin, and Trinidad; C, close-up of the ABC islands north of Venezuela: Aruba, Bonaire, and Curaçao; D, count of confirmed (grey bars) and indeterminate (black bars) number of families, genera, and species of fossil anomurans and brachyurans for each of the countries, states, territories, or islands included in this study.

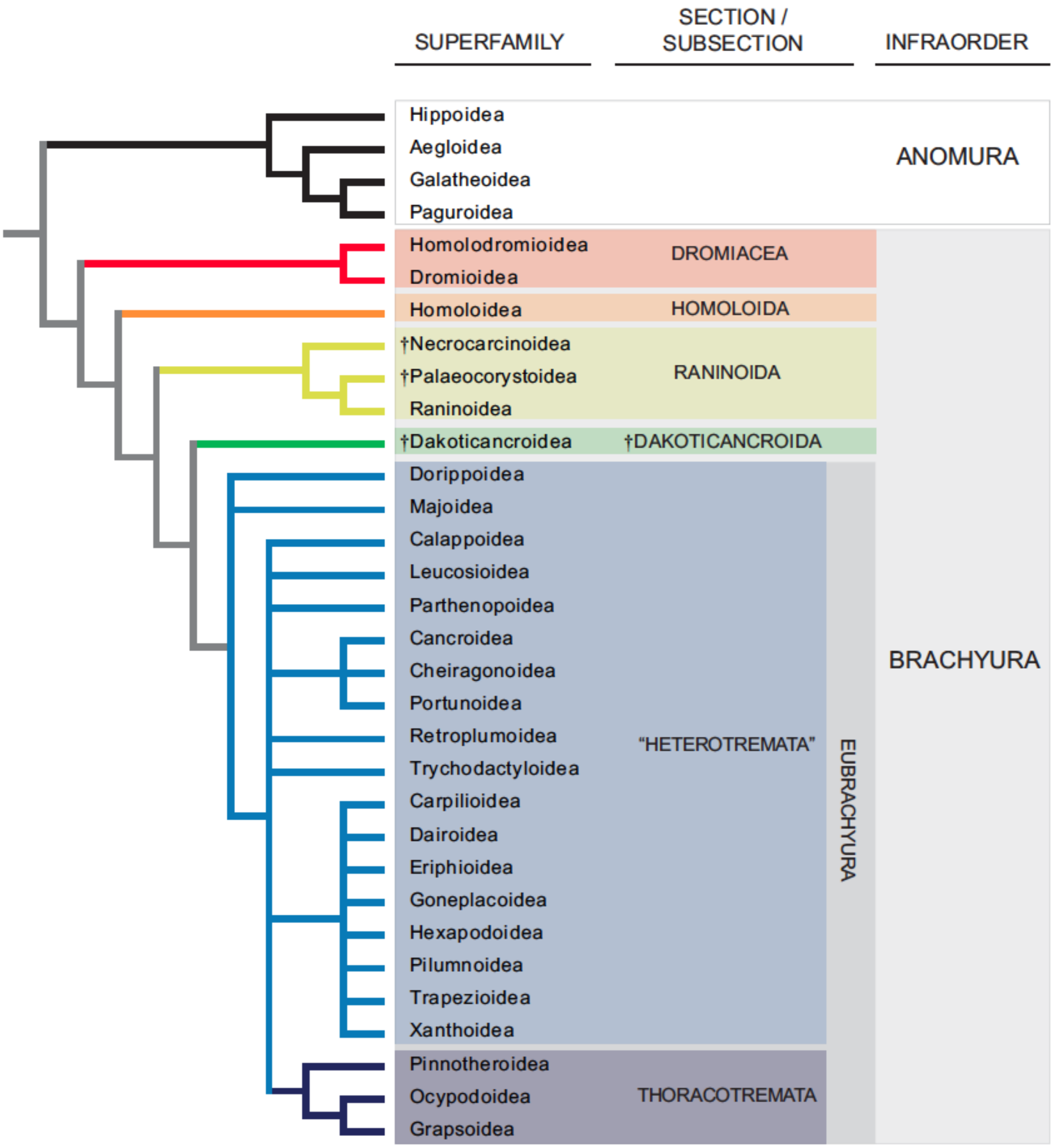


Figure 5.2. Schematic phylogenetic relationships among the superfamilies of Anomura and Brachyura listed in this work. The general topology and colored boxes reflect current phylogenetic scenarios based on molecular and morphological data, partially following the works of Bracken-Grissom *et al.* (2013) for Anomura (white box), Karasawa *et al.* (2011) for podotremous Brachyura (colored boxes), and Tsang *et al.* (2014) for some eubrachyuran Brachyura (grey box). The order in which superfamilies are listed in this figure, from top to bottom, is the same followed through the checklist and in Figure 5.17, whereas families, genera, and species within a given superfamily are listed alphabetically. Superfamilies with a dagger (†) are only known from fossils.

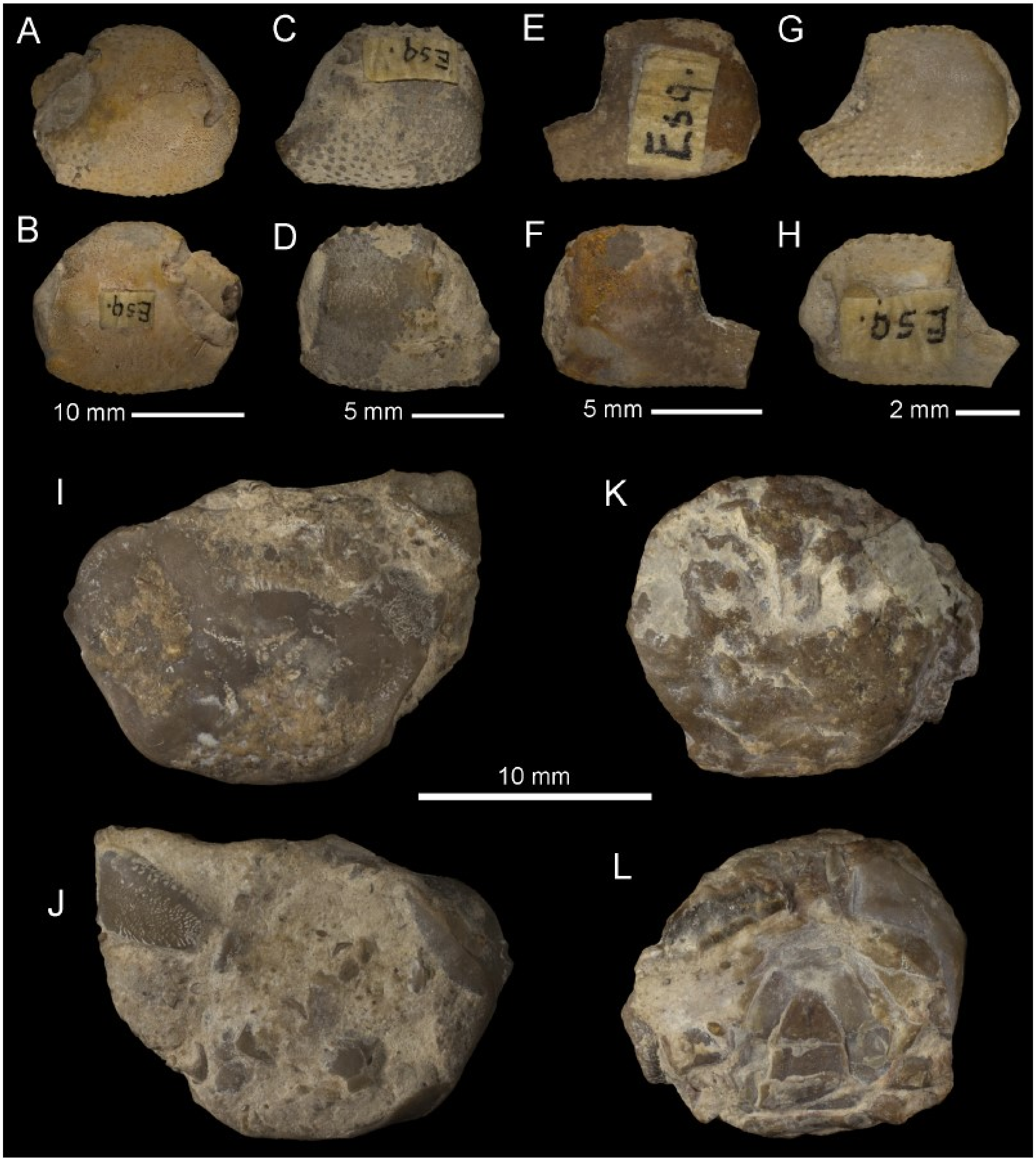


Figure 5.3**.** Fossil Anomura and Brachyura from the Cretaceous of Bolivia, South America. A–H, Anomura: Paguroidea: ?Diogenidae, Cenomanian of Potosí; A–B, MNHN-F.A57970, left cheliped in outer (A) and inner (B) views; C–D, MNHN-F.A57972, left cheliped in outer (C) and inner (D) views; E–H, MNHN-F.A57971, left chelipeds in outer (E, G) and inner (F, H) views. I–L, Brachyura: Eubrachyura, of Potosí; I–J, eubrachyuran indet., MNHN-F.A57973, in dorsal (I) and ventral (J) view. K–L, eubrachyuran indet., MNHN-F.A57966, in dorsal (K) and ventral (L) view. Photos courtesy of Jocelyn Falconnet, Peter Massicard, and Sylvain Charbonnier (MNHN). All specimens dry, uncoated.

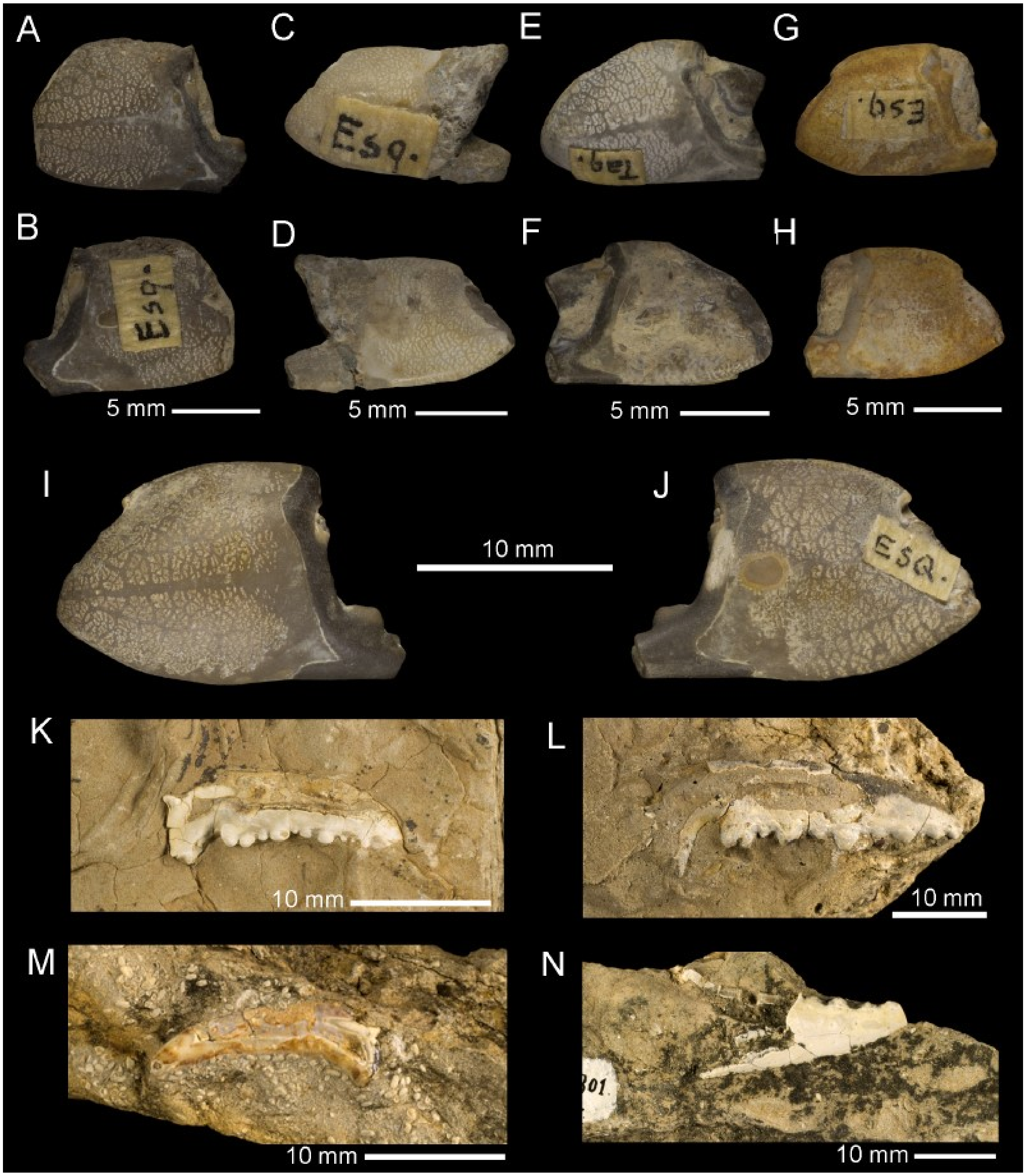


Figure 5.4**.** Fossil Brachyura from the Cretaceous and Neogene of Bolivia, South America. A–J, eubrachyuran chelipeds associated with crab carapace MNHN-F.A57966 (see Fig. 5.3K, L) from the Cenomanian of Potosí; A–H, MNHN-F.A57968, several right chelipeds in outer (A, C, E, G) and inner (B, D, F, H) views; I–J, MNHN-F.A57967, a large right cheliped in outer (I) and inner (J) view. K–N, eubrachyuran chelipeds from the Miocene of Santa Cruz; K, MNHN-F.A57963, dactylus; L, MNHN-F.A57961, dactylus; M, MNHN-F.A57962, dactylus; N, MNHN-F.A57964, fragment of pollex. Photos courtesy of Jocelyn Falconnet, Peter Massicard, and Sylvain Charbonnier (MNHN). All specimens dry, uncoated.

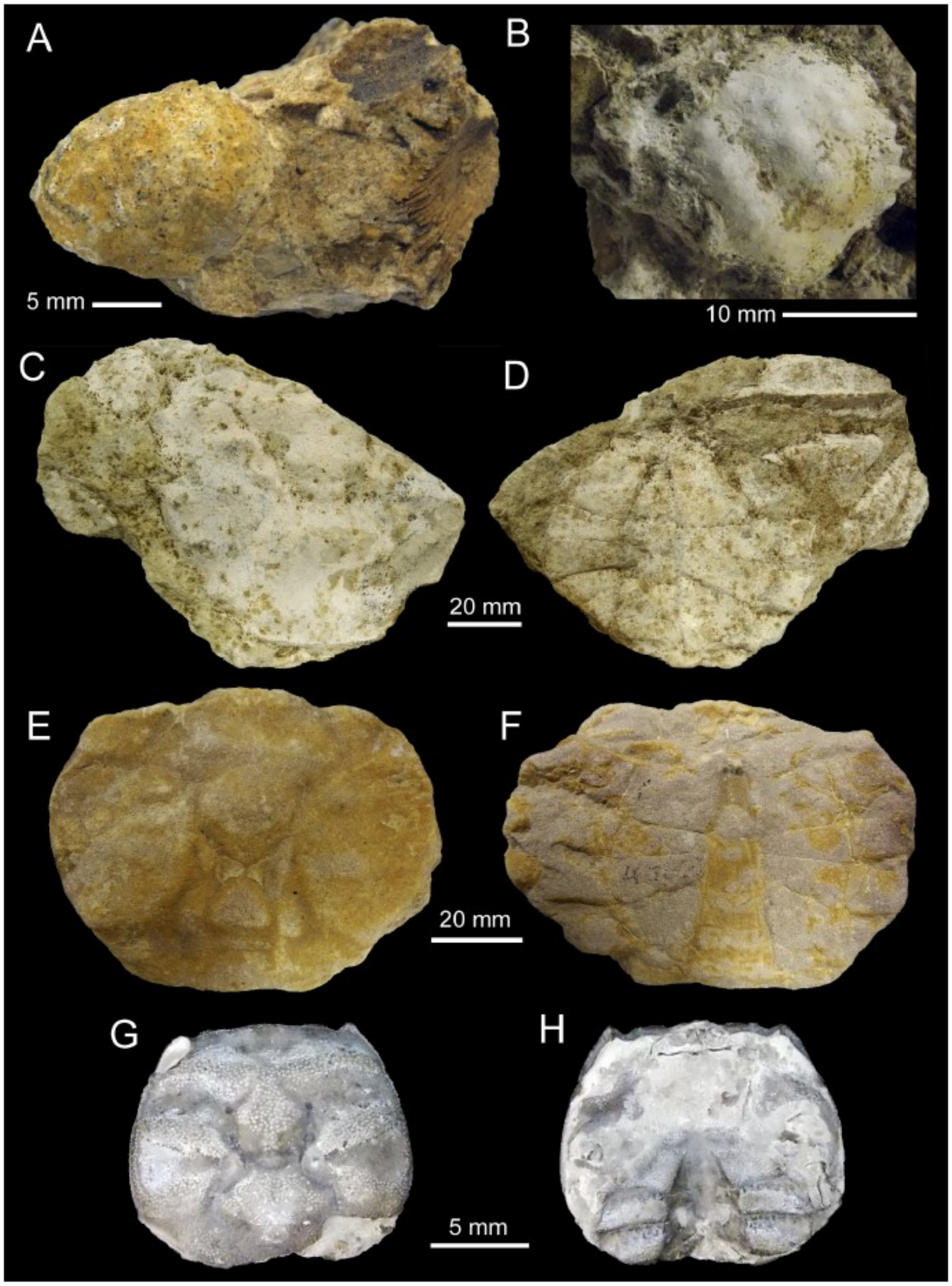


Figure 5.5. Fossil Eubrachyura from the Cretaceous of Brazil, South America. A–B, Calappoidea: Calappidae: A, *Acanthocarpus obscurus* **(**Rathbun, 1918) MNRJ 4583-I, carapace, dorsal view, early Miocene of Pará; B, *Calappa circularis* (Beurlen, 1958a), syntype, MNRJ 4619-I, carapace, dorsal view, Miocene of Pará. C–D, Portunoidea: Portunidae: *Callinectes paraensis* Beurlen, 1958a, male, holotype, MNRJ 4585-I, early Miocene of Pará, dorsal (C) and ventral (D) views. E–F, Macropipidae: *Ophtalmoplax brasiliana* (Maury, 1930), male, MNRJ 4581-I, Maastrichtian of Paraíba, dorsal (E) and ventral (F) views. G–H, Retroplumoidea: Retroplumidae: *Costacopluma nordestina* Feldmann and Martins Neto, 1995, male, LPURCA specimen uncatalogued, Paleocene of Pernambuco, dorsal (G) and ventral (H) views. Photos by William Santana. All specimens dry, uncoated.

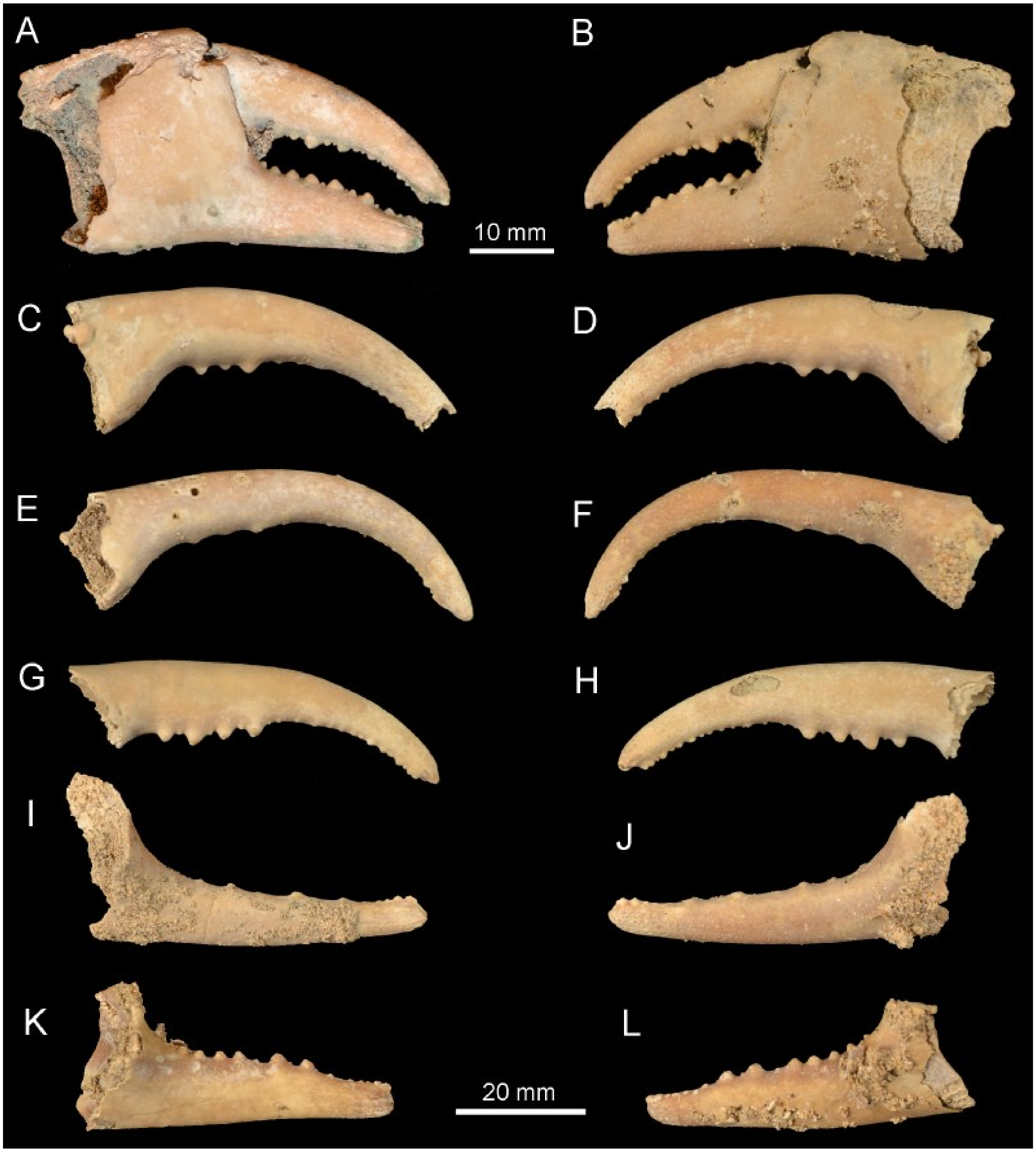


Figure 5.6. Fossil Eubrachyura from the Pleistocene of Brazil, South America. A–L, Grapsoidea: Gecarcinidae: *Johngarthia lagostoma* H. Milne Edwards, 1837, USNM 618300, Pernambuco; A–B, articulated minor cheliped; C–H, isolated dactyli of major cheliped; K–L, isolated/fragmented major cheliped pollices. Photos by Javier Luque. All specimens dry, uncoated.

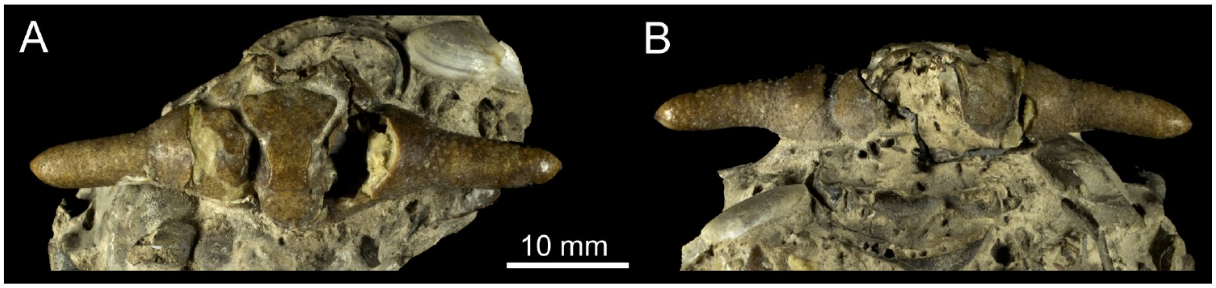


Figure 5.7. Fossil Eubrachyura from the Cenozoic of Chile, South America. A–B, Leucosoidea: Leucosidae: *Ixa* sp. cf. *I. cylindrus* (Fabricius, 1777), MNHN-F.R03449, Cenozoic indet., locality unknown, in dorsal (A) and frontal (B) views. Photos courtesy of Peter Massicard and Sylvain Charbonnier (MNHN). All specimens dry, uncoated.

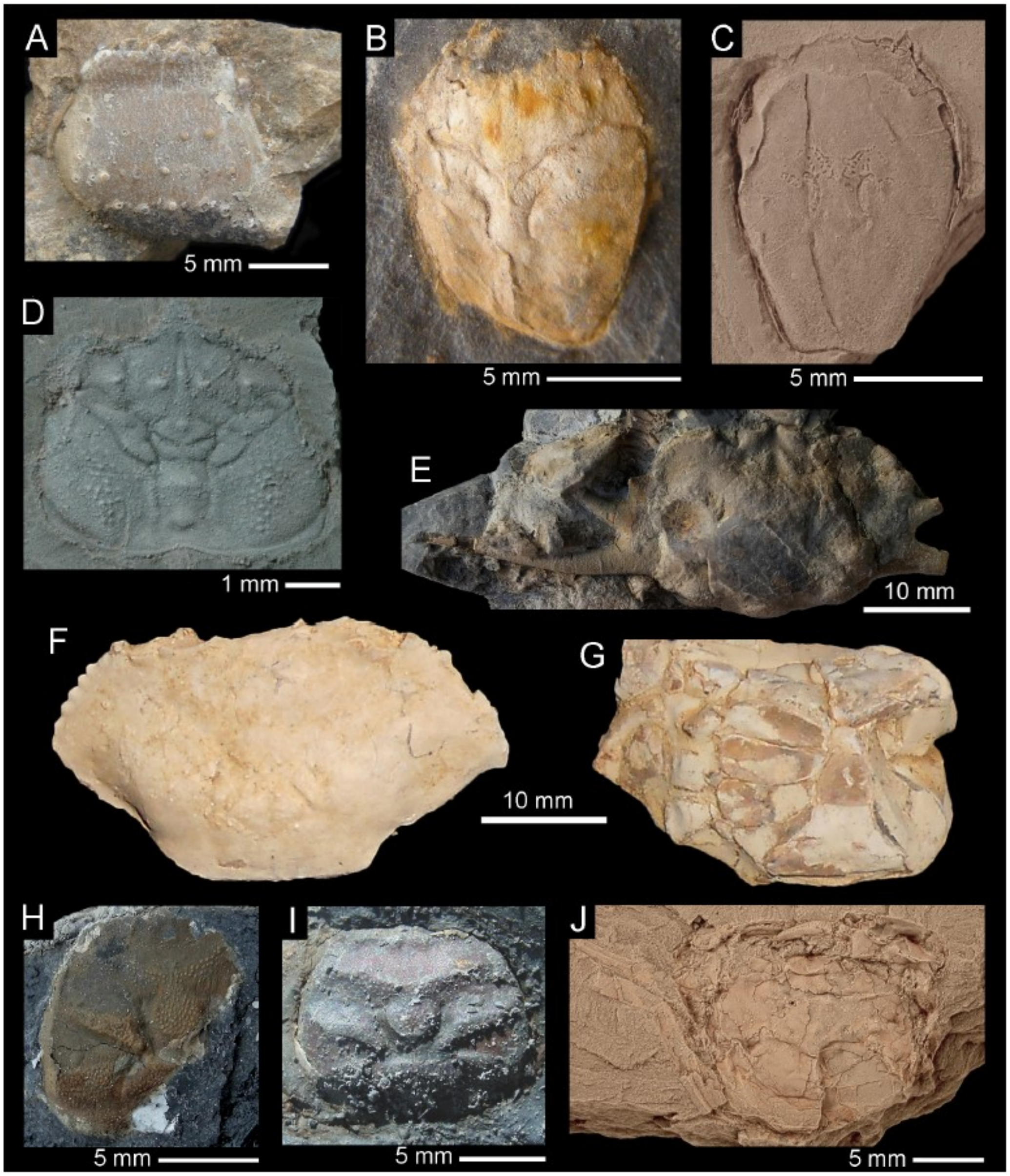


Figure 5.8. Fossil Anomura and Brachyura from the Cretaceous and Cenozoic of Colombia, South America. A, Anomura: Paguroidea: Diogenidae: ?*Paguristes* sp. left cheliped, specimen IGM p880851, late Valanginian, Santander. B–J, Brachyura; B–C, Raninoida; B, Palaeocorystoidea: Palaeocorystidae: *Joeranina kerri* (Luque *et al.*, 2012), dorsal view of holotype IGM p881128, late Aptian of Santander; C, Raninoidea: Raninidae: Raninoidinae: *Quasilaeviranina* sp., dorsal view of uncatalogued specimen, early-middle Santonian of Boyacá; D–J, Eubrachyura; D, Dorippoidea: Telamonocarcinidae: *Telamonocarcinus antiquus* Luque, 2015a, dorsal view of holotype IGM p881012, early Albian of Santander. E, Carpilioidea: Palaeoxanthopsidae: *Palaeoxanthopsis* sp., dorsal view of specimen IGM IGM p881293, Maastrichtian of Santander. F, G, Portunoidea: Portunidae: Portuninae: *Portunus oblongus* Rathbun, 1920b, from the Miocene of La Guajira; F, dorsal view, specimen MUN-STRI 37322; G, male ventral view, specimen MUN-STRI 37324. H, I, Retroplumoidea: Retroplumidae: *Costacopluma* sp. from the Maastrichtian of Santander; H, dorsal carapace, specimen IGM p881282; I, dorsal carapace, specimen IGM p881282. J, Eubrachyura *incertae sedis*, dorsal view of specimen IGM p881262, Paleocene of La Guajira. Photos by Javier Luque. Specimens C, D, J dry, coated with ammonium chloride; all other specimens dry, uncoated.

Figure 5.9. Fossil Eubrachyura from the Cenozoic of Peru, South America. A, B, Cancroidea: Cancridae: *Cancer borealis* Stimpson, 1859, early Pliocene of Pisco, dorsal view of specimens MNHN.F.R07746 (A) and MNHN.F.R07748 (B). C, Majoidea: Majidae: Epialtinae: *Eoinachoides latispinosa* Carriol, Carriol, Muizon and Secretán, 1987, late Miocene of Pisco, holotype, MNHN.F.R70743, dorsal view. D, E, Portunoidea: Geryonidae: *Chaceon peruvianus* (d'Orbigny, 1842), Miocene of Sasaco (locality unknown), holotype, MNHN.F.B33420, dorsal (D) and ventral (E) views. F–H, Portunidae: Podophthalminae: ?*Euphylax* sp., Eocene of Pisco, specimen USNM 618318, dorsal view (F); specimen USNM 618319a, dorsal view (G); specimen USNM 618319b, ventral view (H). I–K, Portuninae: *Callinectes* sp. aff. *C. reticulatus* Rathbun, 1918, middle ?Oligocene of Piura, specimen USNM 496112a, dorsal (I) and frontal (J) views; specimen USNM 496112b, dorsal view (K). Photos A–D courtesy of Jocelyn Falconnet, Peter Massicard, and Sylvain Charbonnier (MNHN); photos F–K by Javier Luque. Specimens A–D dry, uncoated; F–K dry, coated with ammonium chloride.

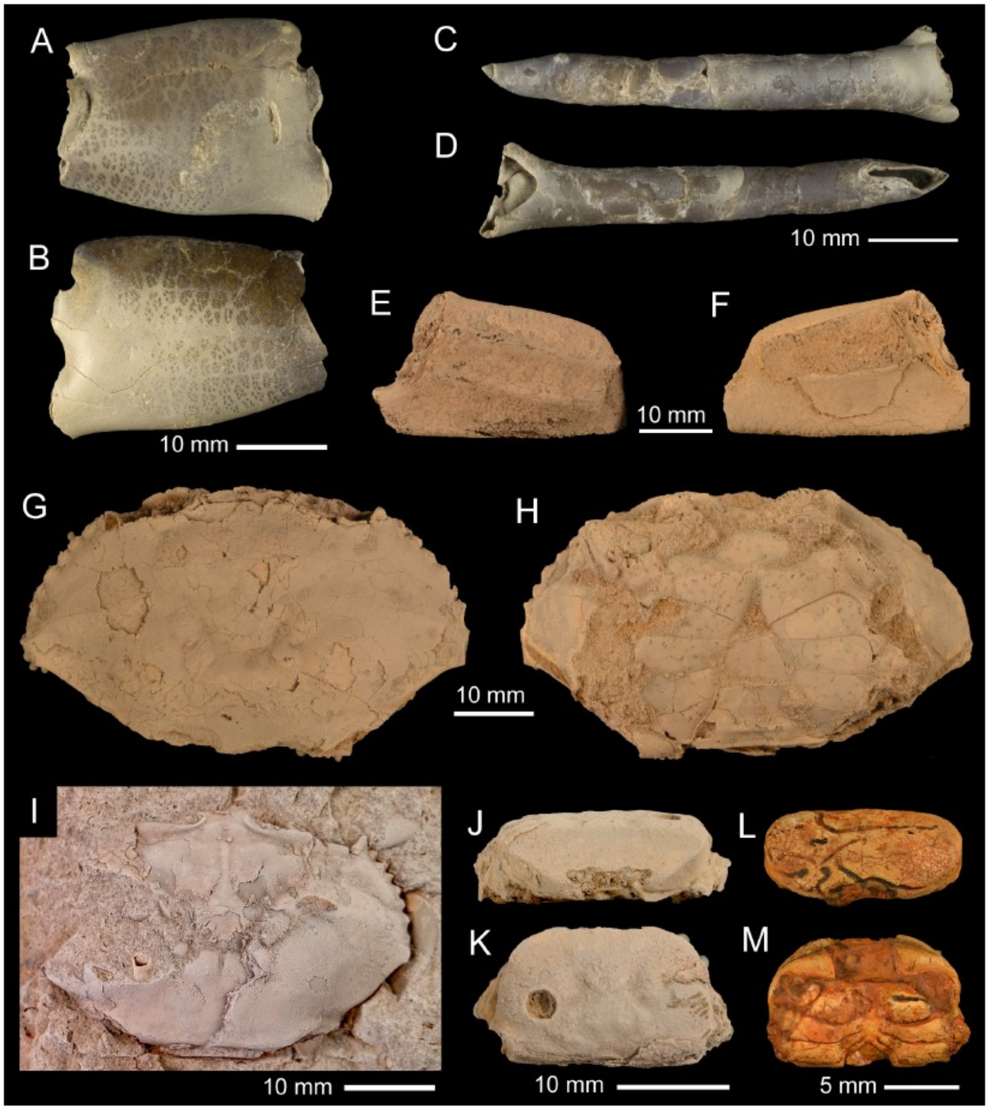


Figure 5.10. Fossil Eubrachyura from the Cenozoic of Peru and Venezuela. A–D, eubrachyuran cheliped remains indet., MNHN-F.A57960, from the late Miocene of El Jahuay, Peru. A, B, left propodus, outer (A) and inner (B) views; C, D, malformed dactylus, upper (C) and lower occlusal (D) views. E–H, Portunoidea: Portunidae: Portuninae: *Callinectes* Stimpson, 1862, from the Miocene of Zulia, Venezuela; E, F, *Callinectes* sp. cf. *C. reticulatus* Rathbun, 1918, left cheliped, USNM 618310, in outer (E) and inner (F) views; G, H, *Callinectes* sp. cf. *C. declivis* Rathbun, 1918, USNM 618306, dorsal carapace in dorsal (G) and ventral (H) views. I, Podophthalminae: *Paraeuphylax cubaensis* Varela and Schweitzer, 2011, USNM 618317, early Miocene of Zulia, Venezuela, dorsal carapace. J–M, Hexapodoidea: Hexapodidae: *Palaeopinnixa* Vía Boada, 1966, from the Miocene of Falcón, Venezuela; J, K, *Palaeopinnixa* sp., USNM 618314, in frontal (J) and dorsal (K) views with a circular hole in left branchial region (see text, Panama, Note 3). L, M, *Palaeopinnixa* sp., USNM 618316, in frontal (L) and ventral (M) views. Photos A–D courtesy of Jocelyn Falconnet, Peter Massicard, and Sylvain Charbonnier (MNHN); photos E–M by Javier Luque. Specimens A–D, L, M dry, uncoated; E–K dry, coated with ammonium chloride.

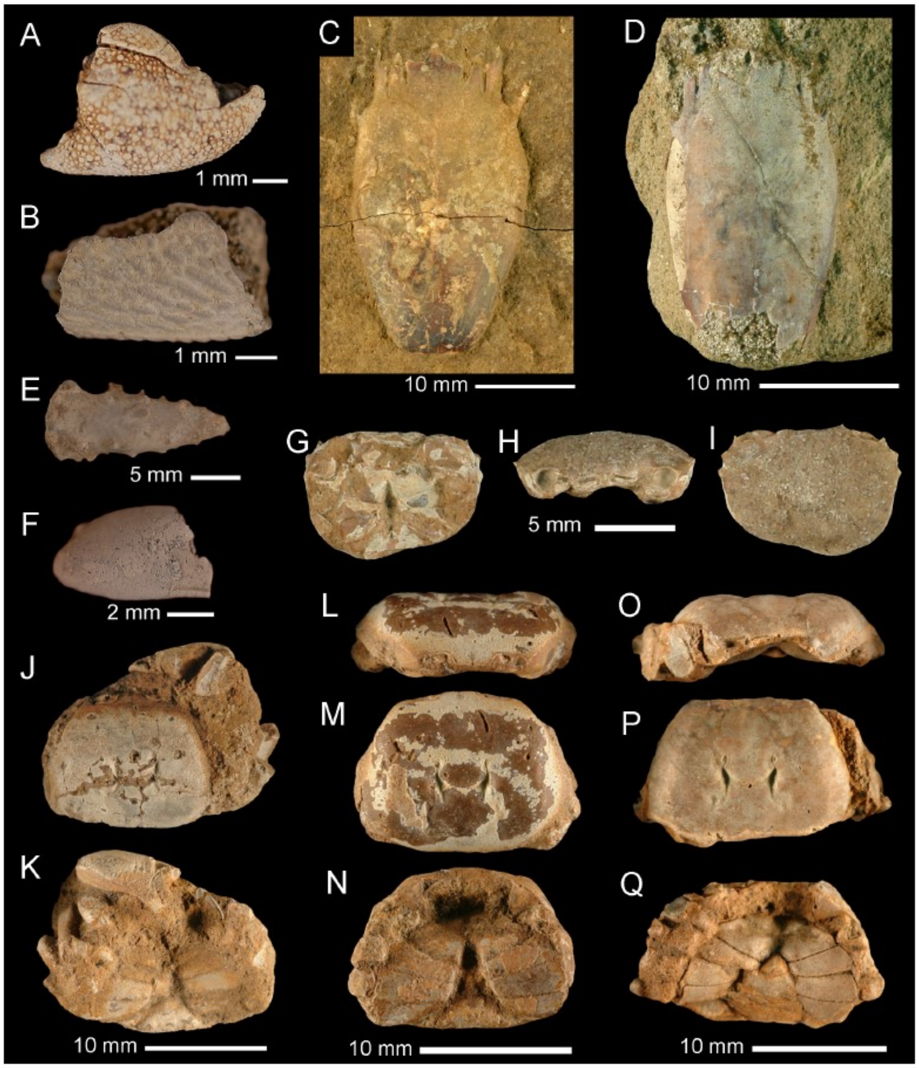


Figure 5.11. Fossil Anomura and Brachyura from Costa Rica and Panama, Central America. A, B, Anomura: Galatheoidea: Porcellanidae: A, *Pachycheles latus* Rathbun, 1918, holotype, USNM 324264, Pliocene of Port Limón, Costa Rica; B, *Petrolisthes avitus* Rathbun, 1918, holotype USNM 324266, Pliocene of Port Limón, Costa Rica. C, D, Brachyura: Raninoidea: Raninidae: Raninoidinae: *Raninoides* sp. cf. *R. benedicti* Rathbun, 1935a, late Miocene of Panama; C, UF 210170, dorsal carapace, Chiriquí; D, UF 274886, dorsal carapace, Colón. E, Dorippoidea: Goniochelidae: *Goniochele armata* Rathbun, 1918, holotype, USNM 324259, dactylus, early Miocene of the Panama Canal. F–I, Goneplacoidea: Euryplacidae; F, *Euryplax culebrensis* Rathbun, 1918, holotype, USNM 324226, right cheliped propodus, early Miocene of the Panama Canal; G–I, *Euryplax* sp., UF 262570, early Miocene of the Panama Canal, in frontal (G), dorsal (H), and ventral (I) views. J–Q, Chasmocarcinidae: *Falconoplax kugleri* Van Straelen, 1933b, early Miocene of the Panama Canal; J, K, UF 260866, in dorsal (J) and ventral (K) views; L–N, UF 262570, in frontal (L), dorsal (M), and ventral (N) views; O–Q, UF 260866, in frontal (L), dorsal (M), and ventral (N) views. Photos A, B, E, F courtesy of Rodney Feldmann (KSU); photos C, D, G–Q courtesy of Sean Roberts (FLMNH). Specimens A, B, E, F dry, coated with ammonium chloride; C, D, G–Q dry, uncoated.

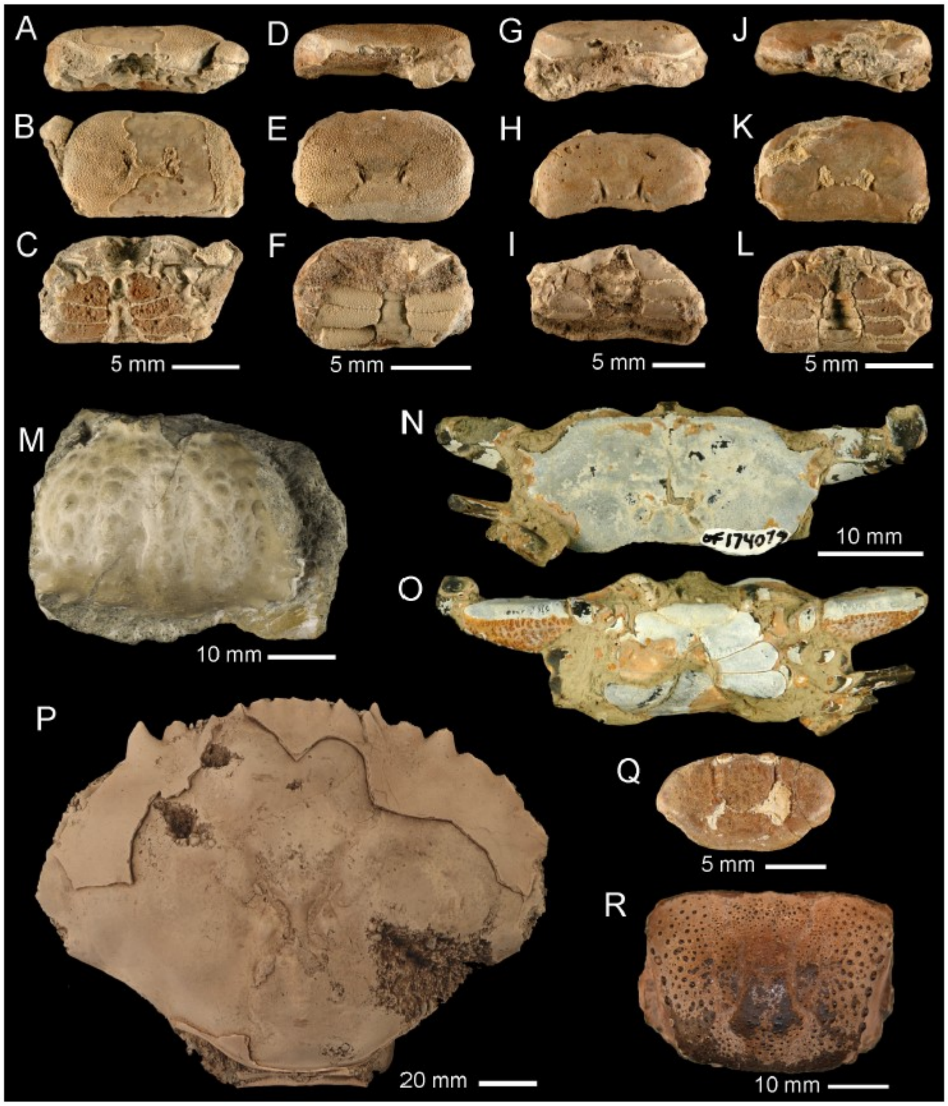


Figure 5.12**.** Fossil Eubrachyura from Panama, Central America. A–L, Hexapodoidea: Hexapodidae: *Palaeopinnixa prima* (Rathbun, 1918), early Miocene of the Panama Canal; A–C, UF 217685; D–F, UF 219754; G–I, UF 219750; J–L, UF 219751; specimens in frontal (A, D, G, J), dorsal (B, E, H, K), and ventral (C, F, I, L) views. M, Calappoidea: Calappidae: *Calappa zurcheri* Bouvier, 1899, holotype, MNHN-F.R03770, dorsal carapace, Miocene of Panama, locality unknown. N, O, Portunoidea: Portunidae: Podophthalminae: ?*Euphylax* sp., UF 174079, Quaternary, Pacific of Panama, dredged from a depth of ~50.0 meters, in dorsal (N) and ventral (O) views. P, Necronectinae: *Necronectes proavitus* (Rathbun, 1918), hypotype, USNM 371312, Miocene of Colón, dorsal carapace. Q, Pinnotheroidea: Pinnotheridae: Pinnotherinae: *Pinnotheres* sp., UF 115397, early Miocene Panama Canal, dorsal carapace. R, Ocypodoidea: Ocypodidae: Ocypodinae: *Uca ornata* Smith, 1870, USNM 618320, Holocene, Pacific of Panama, dorsal carapace. Photos A–L, N, O courtesy of Sean Roberts (FLMNH); photo M courtesy of Jocelyn Falconnet, Peter Massicard, and Sylvain Charbonnier (MNHN); photos P–R by Javier Luque. Specimens A–O, Q, R dry, uncoated; P dry, coated with ammonium chloride.

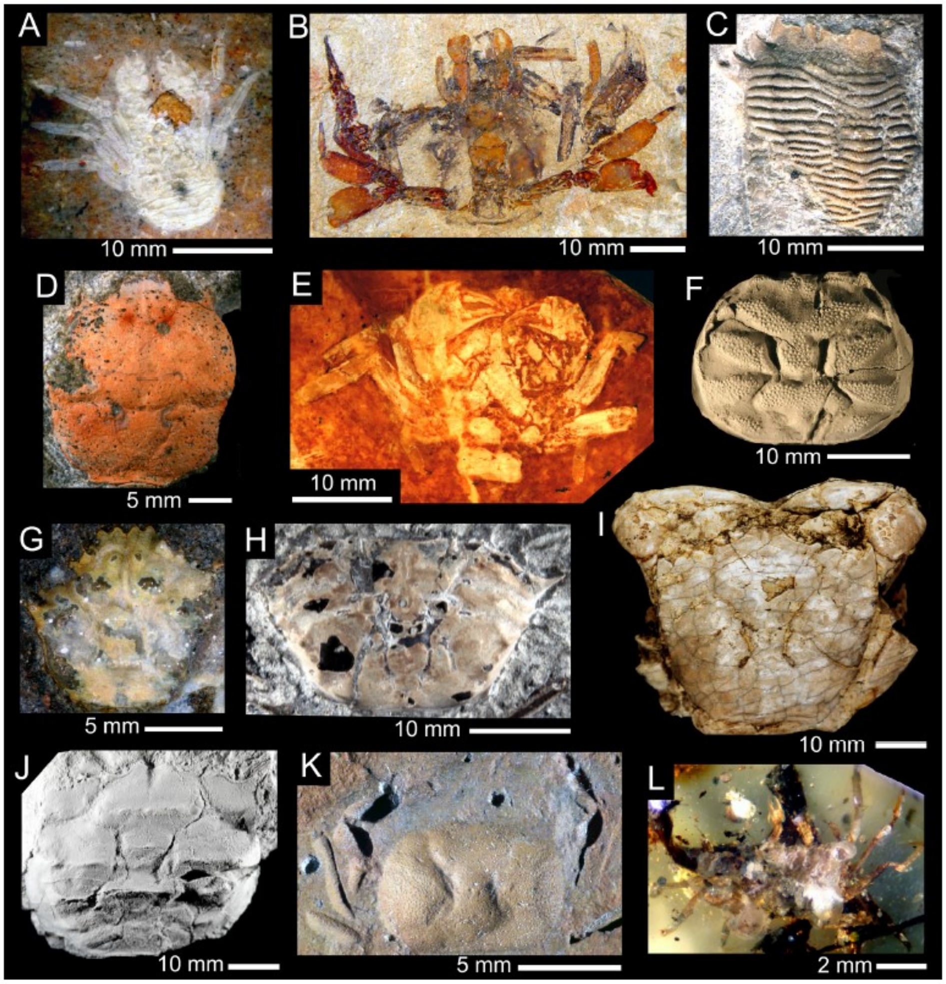


Figure 5.13. Fossil Anomura and Brachyura from Mexico. A, Anomura: Aegloidea: Aeglidae: *Protaegla minuscula* Feldmann, Vega, Applegate and Bishop, 1998b, holotype, IGM-6502, late Albian of Puebla. B–L, Brachyura. B, Necrocarcinoidea: Cenomanocarcinidae: *Cenomanocarcinus vanstraeleni* Stenzel, 1945, hypotype, MUZ-801, Turonian of Múzquiz, Coahuila; C, Raninoidea: Raninidae: *Lophoranina cristaspina* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001a, hypotype, IHNFG-3460, middle Eocene of Copoya, Chiapas; D, Dakoticancroidea: Ibericancridae: *Sodakus mexicanus* Vega, Feldmann and Villalobos-Hiriart, 1995b, hypotype to be deposited at CPC, early Maastrichtian of Paredón, Coahuila; E, Superfamily uncertain: Tepexicarcinidae: *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate and Bishop, 1998b, hypotype, IGM-6609, late Albian of Puebla; F, Retroplumoidea: Retroplumidae: *Costacopluma mexicana* Vega and Perrillat, 1989, holotype, IGM-4128, early Maastrichtian of Sierra El Antrisco, Nuevo León, Mexico; G, Cheiragonoidea: Cheiragonidae: *Karasawaia markgrafi* (Lőrenthey, 1907 [1909]), hypotype, IHNFG-3030, early Eocene of El Veinte, Chiapas; H–J, Portunoidea; H, Icriocarcinidae: *Icriocarcinus xestos* Bishop, 1988, hypotype, IGM.6625-2, late Campanian of Punta Santo Tomás, Baja California; I, Carcineretidae: *Carcineretes planetarius* Vega, Feldmann, Ocampo and Pope, 1997, hypotype, IHNFG-3412, early Maastrichtian of Ocozocoautla, Chiapas; J, Macropipidae: *Ophthalmoplax brasiliana* (Maury, 1930), hypotype, CPC-881, late Maastrichtian of Arroyo Amargos, Coahuila; K, ?Pinnotheroidea: ?Pinnotheridae: *Viapinnixa perrilliatae* Vega, Nyborg, Fraaye and Espinosa, 2007a, paratype, IGM-9109, middle Paleocene of La Mesita, Coahuila; L, Grapsoidea: Sesarmidae indet., specimen IHNFG-4991, early Miocene of Simojovel, Chiapas. Photos by Francisco Vega. F and K previously illustrated *in* Armstrong *et al.* (2009), and J *in* Vega *et al.* (2013). Specimens A–E, G–I, K, L dry, uncoated; F and J dry, coated with ammonium chloride.

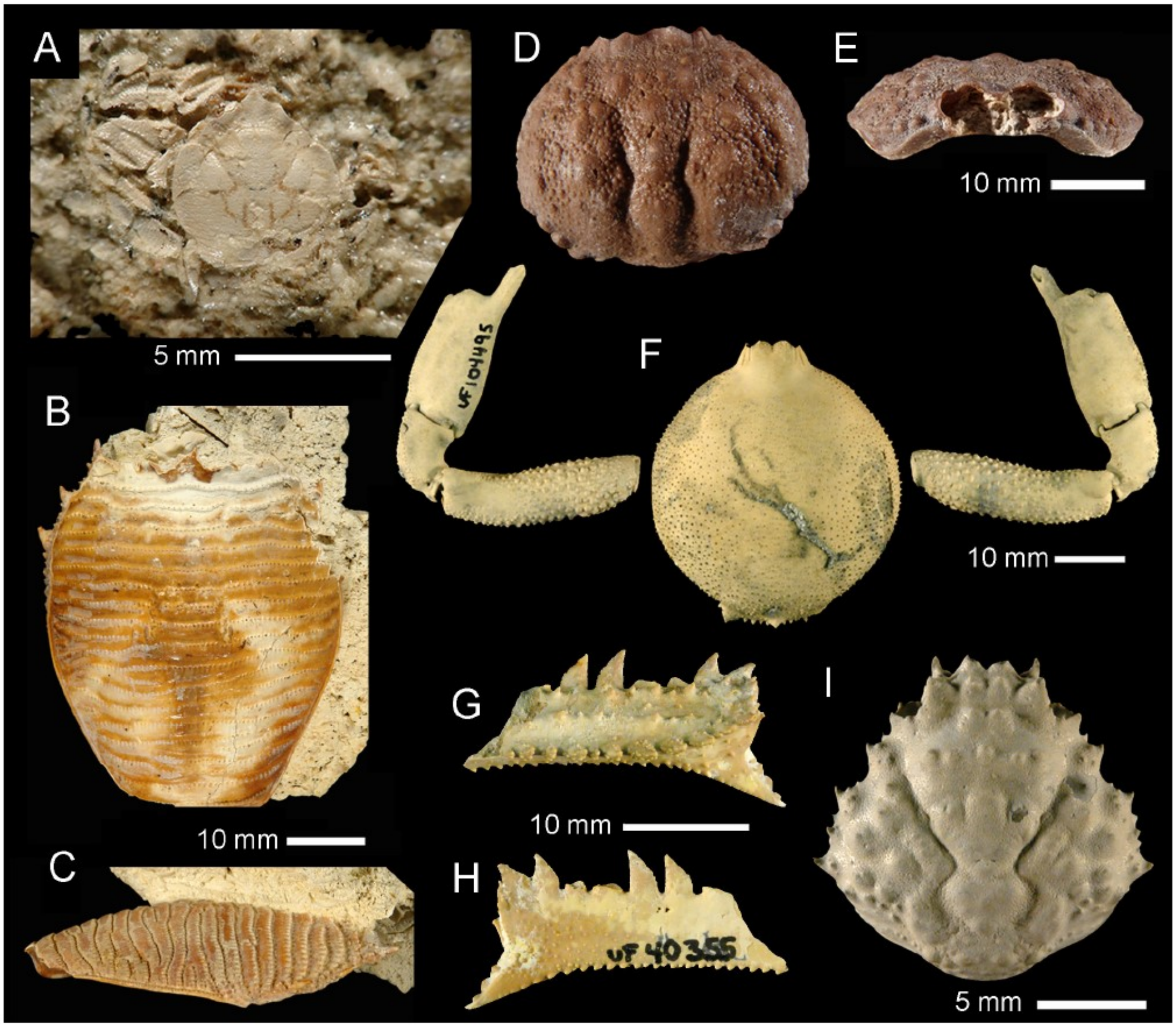


Figure 5.14. Fossil Anomura and Brachyura from southern central and central Florida. A, Anomura: Galatheoidea: Porcellanidae: *Petrolisthes myakkensis* Bishop and Portell, 1989, dorsal view of carapace of holotype UF 8678 adhered to *Heliaster microbrachius* (sun star), late Pliocene of El Jobean, Charlotte County. B, C, Brachyura: Raninoidea: Raninidae: *Lophoranina* sp. cf. *L. georgiana* (Rathbun, 1935), interior and lateral views of dorsal carapace of UF 67098, late Eocene of Ocala, Marion County. D, E, Eubrachyura: Calappoidea: Calappidae: *Calappilia brooksi* Ross and Scolaro, 1964, dorsal (D) and frontal (E) views of UF 13349, late Eocene of Newberry, Alachua County. F, Leucosioidea: Leucosiidae: *Persephona mediterranea* (Herbst, 1794), dorsal view of carapace and interior and exterior views of associated left cheliped UF 104495, early–middle Pleistocene of Fort Drum, Okeechobee County. G, Majoidea: Mithracidae: *Damithrax* sp. cf. *D. pleuracanthus* (Stimpson, 1871), dorsal view of carapace of hypotype UF 29057, Pliocene–Pleistocene of Sarasota, Sarasota County. H, I, Parthenopoidea: Parthenopidae: *Platylambrus charlottensis* (Rathbun, 1935), external and internal views of right propodus UF 40355, Arcadia, De Soto County. Photos courtesy of Sean Roberts (FLMNH). All specimens dry, uncoated.

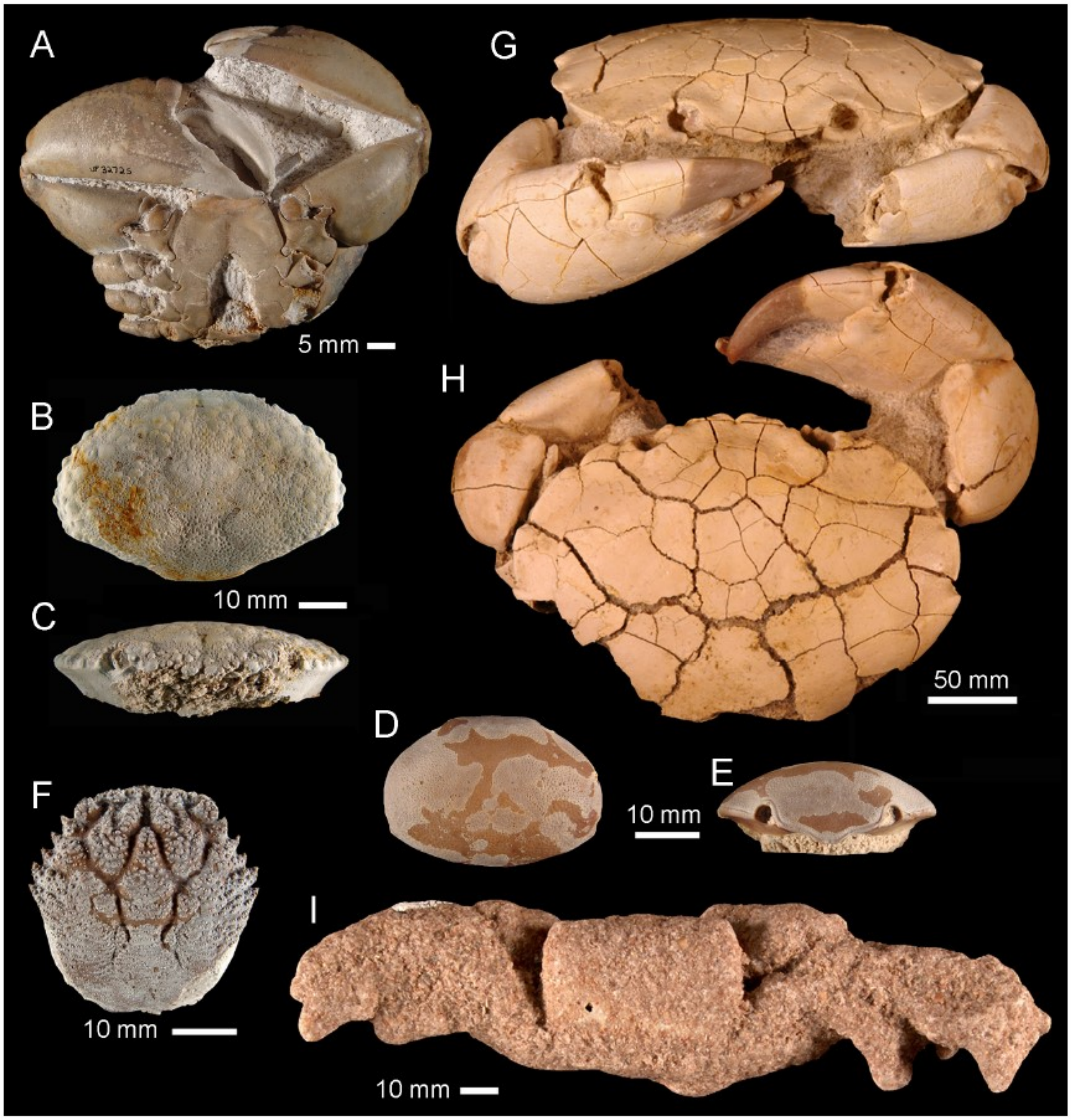


Figure 5.15. Fossil Eubrachyura from southern and central Florida. A, Carpilioidea: Carpiliidae: *Ocalina floridana* Rathbun, 1929, ventral view of UF 32725, late Eocene of Newberry, Alachua County; B, C, dorsal (B) and frontal (C) views of UF 105902, Newberry, Alachua County. D, E, *Palaeocarpilius brodkorbi* Lewis and Ross, 1965, dorsal (D) and frontal (E) views of UF 114368, late Eocene of Newberry, Alachua County. F, Cheiragonoidea: Cheiragonidae: *Montezuemella microporosa* Portell and Collins, 2002, dorsal view of holotype UF 107150, late Eocene of Newberry, Alachua County. G, H, Eriphioidea: Menippidae: *Menippe mercenaria* (Say, 1818), dorsal (H) and frontal (G) views of carapace UF 24668, late Pleistocene of Oldsmar, Pinellas County. I, Ocypodoidea: Ocypodidae: *Ocypode quadrata* (Fabricius, 1787), dorsal view of carapace, hypotype, UF 47573, late Pleistocene–Holocene of Satellite Beach, Brevard County. Photos courtesy of Sean Roberts (FLMNH). All specimens dry, uncoated.

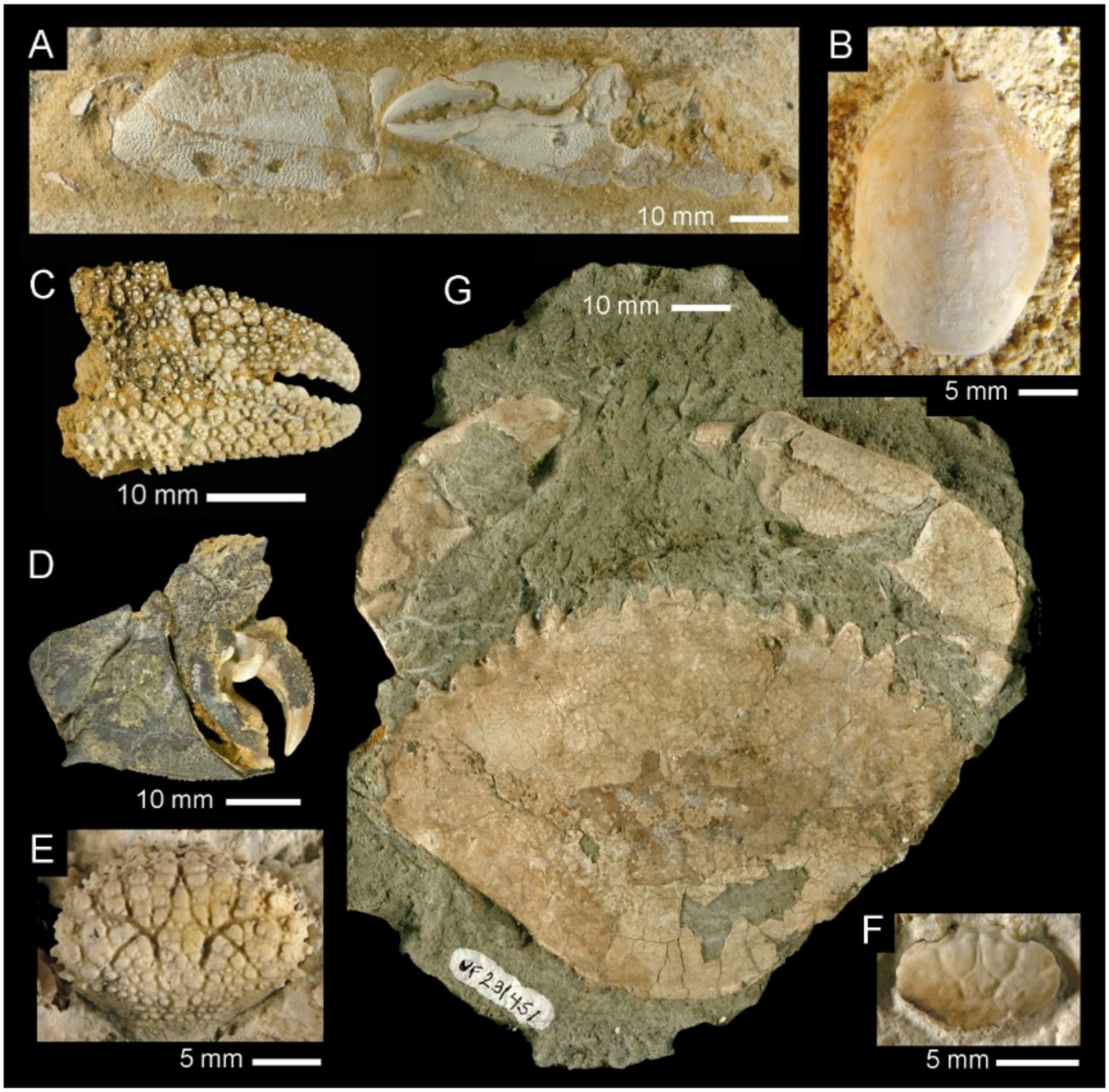
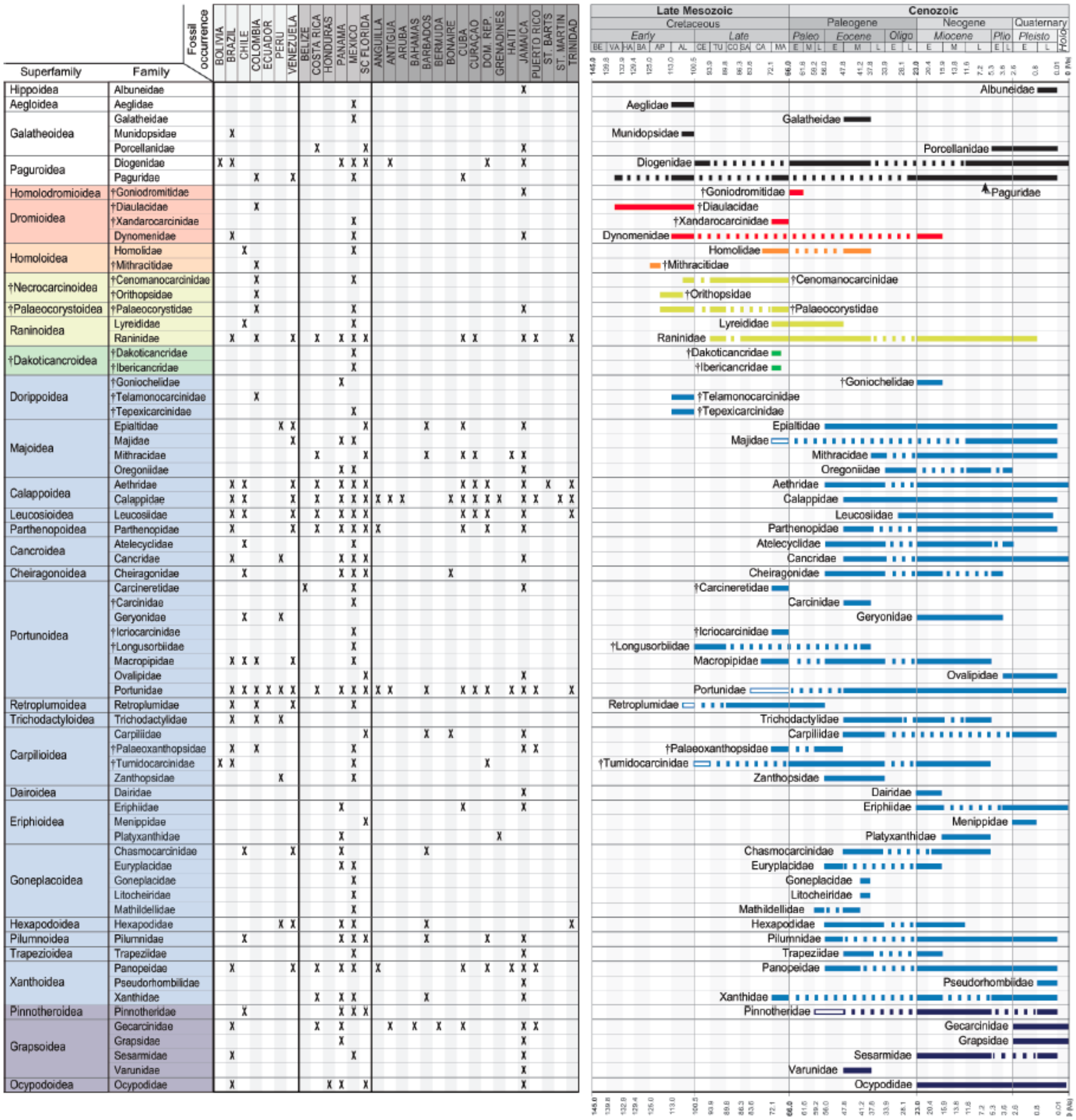


Figure 5.16. Fossil Anomura and Brachyura from the Neogene of the Caribbean. Antigua: A, Brachyura: Portunoidea: Portunidae: *Necronectes summus* Collins and Donovan, 1995, external view of chelipeds UF 242593 embedded in limestone, Free Town, parish of Saint Thomas. Curaçao: B, Brachyura: Raninoidea: Raninidae: *Ranilia constricta* (Milne-Edwards, 1880b), dorsal view of carapace UF 227321, Saint Michiel. Jamaica: C, Anomura: Paguroidea: Diogenidae: *Petrochirus bahamensis* (Herbst, 1791), external view of right fixed finger and dactylus of UF 273849, Fort, parish of St. Thomas. D, Brachyura: Calappoidea: Calappidae: *Calappa springeri* Rathbun, 1931, external view of right carpus, propodus, and dactylus of UF 273851, Fort, parish of St. Thomas. E, Dairoidea; Dairidae: *Daira vulgaris* Portell and Collins, 2004, dorsal view of carapace, holotype, UF 68349, Duncans, parish of Trelawny. F, Xanthoidea: Panopeidae: *Lophopanopeus corallines* Portell and Collins, 2004, dorsal view of carapace, holotype, UF 106702, Duncans, parish of Trelawny. Puerto Rico: G, Portunoidea: Portunidae: *Necronectes collinsi* Schweitzer *et al.*, 2006c, dorsal view of carapace, UF 231451, San Sebastian. Photos courtesy of Sean Roberts (FLMNH). All specimens dry, uncoated.

Table 5.1. Geographic (left) and stratigraphic (right) distribution of 32 superfamilies and 69 families of anomurans and brachyurans with fossil records in tropical America summarized in this work. Colors for countries/regions as in Fig. 5.1. Colors for families and superfamilies as in Fig. 5.2. Fossil occurrences for a given family and country are marked with 'X'. Solid horizontal bars indicate the known chronologic and stratigraphic ages for a given family, dotted lines indicate unknown but expected occurrences, and outlined white bars indicate taxa with dubious or indeterminate familial placement. Taxa marked with a dagger (†) only known from fossils. Numerical ages given in millions of years (Ma). Geologic time abbreviations: AL = Albian, AP = Aptian, BA = Barremian, BE = Berriasian, CA = Campanian, CE = Cenomanian, CO = Coniacian, E = early, HA = Hauterivian, Holo = Holocene, L = late, MA = Maastrichtian, M = middle, Oligo = Oligocene, Paleo = Paleocene, Pleisto = Pleistocene, Plio = Pliocene, SA = Santonian, TU = Turonian, VA = Valanginian. Geologic time slices not to scale.



Superfamily	Family	Fossil occurrence																													
		BOLIVIA	BRAZIL	CHILE	COLOMBIA	ECUADOR	PERU	VENEZUELA	BELIZE	COSTA RICA	HONDURAS	PANAMA	MEXICO	SC FLORIDA	ANGUILLA	ANTIGUA	ARUBA	BAHAMAS	BARBADOS	BERMUDA	BONAIRE	CUBA	CURAÇAO	DOM. REP.	GRENADINES	HAITI	JAMAICA	PUERTO RICO	ST. BARTS	ST. MARTIN	TRINIDAD
Hippoidea	Albuneidae																										X				
Aegloidea	Aeglidae												X																		
Galatheoidea	Galatheidae												X																		
	Munidopsidae		X																												
	Porcellanidae									X				X													X				
Paguroidea	Diogenidae	X	X									X	X	X		X								X			X				
	Paguridae				X			X					X									X									
Homolodromioidea	†Goniodromitidae																										X				
Dromioidea	†Diaulacidae				X																										
	†Xandarocarcinidae												X																		
	Dynomenidae		X										X														X				
Homoloidea	Homolidae			X									X																		
	†Mithracitidae				X																										
†Necrocarcinoidea	†Cenomanocarcinidae				X								X																		
	†Orithopsidae				X																										
†Palaeocorystoidea	†Palaeocorystidae				X								X														X				
Raninoidea	Lyreididae			X									X																		
	Raninidae		X		X			X		X		X	X	X								X	X				X	X			X
†Dakoticancroidea	†Dakoticancridae												X																		
	†Ibericancridae												X																		
Dorippoidea	†Goniochelidae											X																			
	†Telamonocarcinidae				X																										
	†Tepexicarcinidae												X																		
Majoidea	Epialtidae						X	X						X					X			X					X				
	Majidae							X				X	X																		
	Mithracidae									X				X					X			X	X			X	X				
	Oregoniidae											X	X														X				
Calappoidea	Aethridae		X	X				X		X		X	X	X								X	X	X			X		X		X
	Calappidae		X	X				X		X		X	X	X	X	X	X				X	X	X	X	X		X	X		X	X
Leucosioidea	Leucosiidae		X	X				X		X		X	X	X								X	X	X			X				X
Parthenopoidea	Parthenopidae		X					X		X		X	X	X	X							X		X			X				
Cancroidea	Atelecyclidae			X									X																		
	Cancridae		X				X					X	X	X													X				
Cheiragonoidea	Cheiragonidae			X								X	X	X							X										
Portunoidea	Carcineretidae								X				X														X				
	†Carcinidae												X																		
	Geryonidae			X			X																								
	†Icriocarcinidae												X																		
	†Longusorbiidae												X																		
	Macropipidae		X	X	X			X					X																		
	Ovalipidae													X													X				
	Portunidae		X	X	X	X	X	X		X		X	X	X	X	X			X			X	X	X		X	X	X			X
Retroplumoidea	Retroplumidae		X		X			X					X																		
Trichodactyloidea	Trichodactylidae		X		X		X																								
Carpilioidea	Carpiliidae													X					X		X						X				
	†Palaeoxanthopsidae		X		X								X														X	X			
	†Tumidocarcinidae	X	X										X											X							
	Zanthopsidae						X						X																		
Dairoidea	Dairidae																										X				
Eriphioidea	Eriphiidae											X										X					X				
	Menippidae													X																	
	Platyxanthidae											X													X						
Goneplacoidea	Chasmocarcinidae			X				X				X							X												
	Euryplacidae											X	X																		
	Goneplacidae												X																		
	Litocheiridae												X																		
	Mathildellidae												X																		
Hexapodoidea	Hexapodidae						X	X				X	X						X												X
Pilumnoidea	Pilumnidae			X								X	X	X					X					X			X				
Trapezioidea	Trapeziidae												X														X				
Xanthoidea	Panopeidae		X					X		X		X	X		X							X		X		X	X	X			
	Pseudorhombilidae																										X				
	Xanthidae									X		X	X						X								X				
Pinnotheroidea	Pinnotheridae			X								X	X	X																	
Grapsoidea	Gecarcinidae		X							X		X				X		X		X		X					X	X			
	Grapsidae											X															X				
	Sesarmidae		X										X														X				
	Varunidae																										X				
Ocypodoidea	Ocypodidae		X								X	X		X													X				

Chapter 6. The eye of the chimaera: Visual systems in fossil and extant podotreme crabs and their phylogenetic implications

6.1. Introduction

The versatility of the brachyuran body plan has allowed this group to radiate and diversify since the Cretaceous, shaping their taxonomic and morphological diversity (Chapter 4). This remarkable diversity of form and function is not restricted to the carapace or limbs, but is also expressed in the their variable compound eye form and underlying visual systems (Cronin and Porter, 2008). Molecular, morphological, larval, and spermatological studies agree on the monophyly of Brachyura (see Chapter 4 and references therein), but the internal classification of the group remains unsettled. Furthermore, little is known about the distribution of visual systems across taxa, in particular in the 'intermediate' podotreme lineages (Fig. 6.1) and visual-system type may assist in understanding the taxonomic classification of the Brachyura. However, the taphonomic preservation of visual features in crab eyes is rare (Klompmaker *et al.*, 2017), and only a handful of fossil specimens preserving corneas and facets are known to date (Vega *et al.*, 2014; Luque, 2015a), obscuring our understanding of the history of visual systems in brachyuran crabs through time.

To better judge the phylogenetic utility of compound eye form for resolving the phylogeny and classification of brachyuran crabs at different ranks, I investigated the distribution of eye types across brachyurans with an emphasis on the problematic 'intermediate' podotreme groups, the center of the disagreement of the main phylogenetic scenarios proposed for Brachyura. I address the following questions: Do closely related taxa with similar ecology share similar underlying visual systems? Are visual systems useful for reconstructing phylogenetic relationships? If so, at what hierarchical levels are they most informative? What does the fossil record tell us about the evolution of visual systems through time?

6.1.1. Basic eye types in crabs

Apposition eyes are the simplest of the compound eye types (Fig. 1.4A). This eye type consists of isolated ommatidia with hexagonal facets that are packed in a hexagonal lattice, and each lense forms an inverted image. It functions best in relatively bright light conditions, and is envisioned as the ancestral condition for crustaceans and present in the larval stages of all decapods (Land, 1980; Fincham, 1984; Porter and Cronin, 2009). The lens systems of eyes of the superposition type (Fig. 1B–C) form together a superimposed erect image. Superposition eyes are better–suited for vision in dim light conditions, and can be recognized by the presence of an "eyeshine" in dark–adapted specimens, and by the presence of a "clear zone" between the outer structures of the eye and the retina (Cronin and Porter, 2008). In parabolic superposition eyes, the sides of the crystalline cones (the structure under each facet of the eye surface) are shaped in the form of a parabola, and the ommatidia may have a lightguide that focuses the collimated light onto the retina (Fincham, 1980; Nilsson, 1989). In refracting superposition eyes (Fig. 1.4B), the crystalline cone contains a refractive index gradient that bends incoming light to focus it on the retina (Nilsson *et al.*, 1986; Nilsson, 1990b). Finally, the reflecting superposition eyes (Fig. 1.4C) lack this refractive index gradient, but instead focus an image by reflecting light off the sides of the crystalline cones as occurs in a mirror box, hence the common name "mirror eyes" (Vogt, 1975; Land, 1976). Facets of this eye type are square instead of hexagonal in cross section. The evolutionary history of apposition and superposition eyes is still poorly understood (Nilsson, 1983; Gaten, 1998). In particular, we lack an understanding of the underlying genetic and developmental mechanisms regulating the expression of a particular eye type in the post-larva. Furthermore, study of fossil crabs with eyes preserved is needed to accurately trace the evolution of eye types across taxa in deep nodes and through time.

6.1.2. Eyes types in larvae and post-larvae

Apposition eyes are found in most larval and adult crustaceans with compound eyes (Gaten, 1998) (Fig. 6.2), suggesting that this eye type is the ancestral condition for the group. However, among non-insect pancrustaceans, reflecting superposition or 'mirror' eyes are unique to post-larva Decapoda (Land, 2000), present in most extant penaeoid and caridean shrimp, lobsters, anomurans such as Galetheoidea and some pylochelideans, and the podotreme brachyurans Dromioidea, Homolodromioidea and Homoloidea (Gaten, 1998; Porter and Cronin, 2009; Scholtz and McLay, 2009). In the Eubrachyura or 'higher' crabs, the loss of reflecting superposition optics via secondary retention of larval apposition eyes appears to have occurred in their most recent common ancestor by progenetic paedomorphosis (Gaten, 1998).

Based solely on the position of sexual openings, taxonomists have traditionally grouped true crabs into Podotremata, Heterotremata, or Thoracotremata (Guinot, 1977) (See Chapter 1, Figure 1.2). This taxonomic grouping presumes that a) Heterotremata and Thoracotremata are monophyletic (together forming the section Eubrachyura), and b) Podotremata, or the 'lower' Brachyura, is monophyletic and sister to Eubrachyura. However, the podotreme condition is plesiomorphic and shared with all anomurans, decapods, and even heterotreme males, casting doubts on its utility for classifying crab taxa, and most phylogenetic studies have recovered a non-monophyletic podotreme grade (see Chapter 4 and references therein). In addition, the distribution of visual systems across brachyuran clades is poorly understood. Ancient podotremes like Homoloidea, Dromiodea, and Homoloidea have 'mirror' eyes — plesiomorphic for crown Decapoda — while eubrachyurans have secondarily retained apposition eyes (Gaten, 1998). Yet, little is known about the eyes types present in 'intermediate' podotreme groups, either fossil or extant (Figure 6.1).

As Gaten (1998) suggested, if the stratigraphic ranges of the fossil and extant decapod crustacean groups is combined with information about their optical types, then some phylogenetical patterns may appear. Herein I present novel data on the optical mechanisms of the puzzling fossil crab †*Callichimaera perplexa* from the Cenomanian–Turonian (95–90 Mya) (Chapter 4), and integrate fossil and extant material from other groups to explore the possibilities and limitations of using fossil compound eyes as an additional tool to enhance our understanding of brachyuran crab evolution through time. As very little is known about the eyes in extant 'intermediate' fossil or extant podotreme brachyurans, the results of this research provide important new insights into the evolution of brachyuran crab eyes, and shed light on the phyletic relationships among primitive and derived brachyuran groups.

6.2. Materials and methods

6.2.1. Materials

Nine specimens of †*Callichimaera perplexa* preserving external and/or internal optical elements (e.g., cornea outline, facets, optic lobe), were collected from the upper Cenomanian–lower Turonian Churuvita Group (95–90 Mya) of Boyacá, Colombia (Chapter 4), and one small fossil specimen of *Cenomanocarcinus* sp. was collected from the upper Coniacian Conejo Formation (85–80 Mya) of Boyacá, Colombia, preserving a small eye with facets. The fossil specimens are deposited in the palaeontological collections of the IGM and MUN-STRI (see list of fossil material studied and associated information in Table 6.1).

Nineteen extant species across all podotreme superfamilies were studied from the invertebrate zoology collections of the USNM, MNHN, and QMW. Specimens were preserved in 70% EtOH, and one eye from selected adult specimens was removed for microscope imaging and preserved in 70%EtOH. Studied taxa include *Dicranodromia felderi* Martin, 1990 (Homolodromioidea: Homolodromiidae); *Dromia personata* (Linnaeus, 1758) and *Hypoconcha* sp. (Dromioidea: Dromiidae), *Dynomene filholi* Bouvier, 1894 (Dromioidea: Dynomenidae); *Homola minima* Guinot and Richer de Forges, 1995*,* and *Latreillopsis bispinosa* Henderson, 1888, (Homoloidea: Homolidae), *Eplumula phalangium* (De Haan, 1839) (Homoloidea: Latreilliidae); *Lysirude nitidus* (A. Milne-Edwards, 1880a) (=*Lyreidus bairdii*), and *Lysirude griffini* Goeke, 1985 (Raninoidea: Lyreididae), *Cyrtorhina granulosa* Monod, 1956, *Symethis* sp., *Cosmonotus grayi* White, 1848; *Notopus dorsipes* (Linnaeus, 1758), *Ranilia muricata* H. Milne Edwards, 1837, *Ranina ranina* (Linnaeus, 1758), *Notopoides latus* Henderson, 1888, *Notosceles viaderi* Ward, 1942, *Raninoides benedicti* Rathbun, 1935a (Raninoidea: Raninidae); and *Clythrocerus nitidus* (A. Milne-Edwards, 1880a) (Cyclodorippoidea: Cyclodorippidae) (see list of extant material studied and associated information is included in Table 6.1).

6.2.2. Methods

6.2.2.1. Tissue processing. Eyes of selected extant adult crabs from museum collections, preserved in 70% EtOH were dissected and prepared for Scanning Electron Microscope (SEM) via dehydration through a series of rinses in EtOH at 70%, 90%, and twice at 100% at intervals of 20 and 30 minutes for small and large samples, respectively. Then the tissues were rinsed for similar time internals in a mixture of of EtOH and Hexamethyldisilazane (HDMS) at 25:75, 50:50, and 75:25 ratios, plus two final rinses in 100% HDMS. This tissue dehydration technique is faster, easier, and cheaper than the critical point drying with CO2.

6.2.2.2. Imaging. For photography of whole specimens, most fossils were coated with sublimated NH_4Cl prior to photographing to enhance relief and fine ornament. Sets of photographs at different focal points were taken with a Nikon Eclipse 80i + Nikon Digital Camera Dxm 1200f, Olympus SZX16® Research Stereomicroscope with a digital camera Qimaging Retiga 2000R Fast 1394, and a Leica Macroscope with Spotflex digital camera. The resulting multi-layered stacks of photos were merged in a single high–definition image using the stacking software Helicon Focus stacking software. Extant specimens were photographed with a Nikon Digital Camera D3100 with MicroNikkor 60 mm and 105 mm lenses.

Dissected and mounted eyes from fossil and extant crabs were studied under Zeiss Scanning Electron Microscope (SEM) Evo 40vp under low vacuum and variable pressure and Back-scattered Electron Detector (BSED) with acceleration voltages of 15 and 20kV, and under a Zeiss Sigma 300 VP-FESEM scanning electron microscope at the Smithsonian Tropical Research Institute, Panama (STRI), and the University of Alberta, Edmonton, Canada. All eye samples from extant taxa were coated with Au/Pd prior to SEM imaging, except from two specimens imaged in a Olympus FV1000 Confocal Microscope. Measurements of cornea dimensions and facet diameters were obtained using ImageJ.

6.3. Results

6.3.1. Eyes of †*Callichimaera perplexa*

†*Callichimaera perplexa* has large globular eyes nearly as wide as long, resting short eyestalks, and lacks orbits, orbital spines, or any protective structures (Figs 6.3, 6.4). The diameter of the cornea measures approximately 15% of the length of the carapace, and is covered by small hexagonal to roundish facets in hexagonal packing with an average diameter of 34 µm Table 6.1). One small specimen (Fig. 6.3A) exhibits a combination of facet shapes and arrays. The central and distal facets are hexagonal to roundish and measure approximately 34 µm in diameter, and are arranged in hexagonal packing (Fig. 6.3C). The proximal facets near the

junction with the podophthalmite are sub-square, measure approximately 26 μm in diameter, and are packed in a somewhat rectilinear array (Fig. 6.3D).

A larger specimen (Fig. 6.3E) has a remarkable preservation of different internal retinal layers (Fig. 6.3F–H). The distal region seems to represent the retina (Fig. 6.3G,H, green). The two most proximal regions are likely homologous with the lamina (Fig. 6.3G,H, blue), and the medulla (Fig. 6.3G,H, red). No lobular neuropills in the eyestalk were recognized.

6.3.2. Eyes of extant podotreme brachyurans

6.3.2.1. Homolodromioidea

Dicranodromia felderi has globular eyes slightly larger than the eyestalk. The podophthalmite is partly covered dorsally in small fine to conical spines, and the eye and eyestalk partially fit a shallow orbit laterally bounded by a short, triangular, anterolaterally diverging outer orbital spine (Fig. 6.5A). In the studied specimen, the corneal eye is nearly as wide as long, its width is approximately 6% the carapace, and is covered on small ommatidia (35 μm) with square facets packed in a rectilinear lattice (Fig 6.5B,C; Table 6.1).

6.3.2.2. Dromioidea

The dromiids *Dromia personata* (Fig. 6.5E,F), *Hypoconcha* sp. (Fig 6. 5G–I), and the dynomenid *Dynomene filholi* (Fig. 6.5J–L) all have eyes with square facets in an orthogonal array. In *Dromia personata*, the eye is small, globular, and about as long as the eyestalk. The podophthalmite is covered with plumose setae, where secondary acicular setae stem form the primary setae (Fig. 6.5E). Its corneal surface is nearly as wide as long, with a width diameter less than 6% the carapace length, and is covered on small rhomboid ommatidia (35 μm) (Fig 6.5F; Table 6.1). In *Hypoconcha* sp., the eyes are also globular, wider than long, and slightly longer than the eyestalk. The cornea has a diameter that is about 9% of the carapace length, and is covered with small rhomboid ommatidia (40 μm) (Fig 6.5H,I). In *Dynomene filholi*, the eyes are small and globular, and shorter than the eyestalk. The podophthalmite is covered with plumose setae, with secondary acicular setae stemming form the primary setae (Fig 6.5K). The cornea has a diameter about 8% the carapace length, and is covered with small square ommatidia (40 µm) with depressed edges (Fig 6.5L).

Square facets packed in an orthogonal lattice have been previously reported for other dromiids and dynomenids such as *Dromia vulgaris* and *Dynomene pilumnoides* (Gaten, 1998; Scholtz and McLay, 2009; Guinot, pers. comm., 2016), supporting the distribution of these features across genera of Homolodromioidea and Dromioidea crabs.

6.3.2.3. Homoloidea

The homolid crab *Homola minima* has hemispherical globular eyes that rest on a slightly longer cylindrical podophthalmite. The basophthalmite is slender, cylindrical, and more than twice as long as the corneal eye or the podophthalmite (Fig. 6.6A). As in other homolids, the podophthalmite rests on a depressed space acting as a false orbit (Davie *et al.*, 2015a). In the studied specimen, the corneal eye is nearly as wide as long, its width is approximately 7% the carapace length, and is covered with small square ommatidia (approx. 30 µm) packed in an orthogonal lattice (Fig 6.6B,C; Table 6.1). Similarly, the homolid *Latreillopsis bispinosa* has a large globular eye with a short podophthalmite and a slender and much longer basophthalmite (Fig. 6.6D). The cornea is smooth, nearly as wide as long, its width is less than 8% the carapace length, and is covered in small square ommatidia (35 µm) packed in an orthogonal lattice (Fig 6.6F; Table 6.1). The boundaries between facets are less conspicuous than in the eye of *Homola minima*, but the overall facet shape and array is still evident above and below the cuticle (Fig 6.6F,G). The latreillid *Eplumula phalangium* has globular eyes, but they rest in shorter podophthalmites compared to the other homoloid species studied. The cornea is wider than it is long, about 13% as wide as the carapace maximum length, and is covered with small square facets (24.5 µm) in rectilinear array.

Similar facet shapes and packing match previous findings for other homoloid taxa such as *Paromola cuvieri*, for which eyes of the reflecting superposition (mirror) type have been reported (Gaten, 1998).

6.3.2.4. Raninoidea

The lyreidid crab *Lyreidus nitidus* (Fig. 6.7A) has small sub-conical eyes resting in stout and much longer podophthalmite, nearly 66% larger than the corneal eye, and covered in fibrous setae (Fig. 6.7B). The eye and eyestalk are partially protected by a narrow orbit with one supraorbital fissure, and a produced, acute, triangular outer orbital spine directed anteromesially. The cornea width is approximately 1.2% the length of the carapace, and is constituted by a few hundred small hexagonal facets that are packed in hexagonal array, with an average facet diameter of 23 µm (Fig. 6.7C; Table 6.1). The studied specimen of *Lysirude griffini* (Fig. 6.7D) has even more reduced sub-conical eyes and a longer and broader podophthalmite than *L. nitidus*; the podophthalmite is nearly twice as long as the corneal eye, and is partly covered in small setae (Fig 7E). Both eye and eyestalk are barely protected by a narrow orbit with one supraorbital fissure, and a short, blunt, triangular outer orbital spine directed anteriorly (Fig 6.7D). The cornea width is approximately 1.5% the length of the carapace, and is constituted by a few hundred small hexagonal facets that are packed in hexagonal array, with an average facet diameter of 23 µm (Fig 6.7C; Table 6.1). Hexagonal facets in hexagonal array have been reported for *Lyreidus tridentatus* (see Scholtz and McLay, 2009), suggesting similar underlying visual systems for the family Lyreididae.

Among all the podotreme crabs studied, those of the family Raninidae have the broadest range of eye shapes, sizes, and orbital constructions. In the subfamily Cyrtorhininae, *Cyrtorhina granulosa* (Fig. 6.7G) shows a considerable reduction of the corneal region compared with the rest of the eyestalk. Its cornea is sub-conical and dorsally truncated by an extension of the cuticle of the podophthalmite that extends towards the pole of the eye, further reducing the area occupied by the cornea (Fig. 6.7H). The cornea width is approximately 1.8% the length of the carapace, and it is constituted by small hexagonal facets in hexagonal array, with an average facet diameter of 35 µm (Fig. 6.7H, I; Table 6.1). The facets across the cornea are similar in size. The cuticular lenses in *C. granulosa* include a thin epicuticle forming the slightly convex outer facets, an underlying thin exocuticle with a concave center, and a membranous underlying endocuticle forming concave facets with raised edges. The podophthalmite is three times larger than the cornea. It is covered in microcuticular tuberculations, and bears multiple setal pits nucleated by a single reduced seta in each. The medial and proximal dorsal portions of the podophthalmite are ornamented with several sub-conical to fungiform nodes ranging in size, the largest of which are capped by an eroded roundish top. Short orbits barely protect the eyes, with a sub-horizontal supraorbital margin bearing two orbital fissures separating the short, blunt, triangular orbital spines.

Species of the subfamily Symethinae have the shortest eyes of all the raninoids studied. In *Symethis* sp. (Fig. 6.7J) the eyestalk is very reduced, and the corneal eye is concealed to a very narrow orbit, considerably restricting the motion of the eye. The cornea maximum width is about 1.4% of carapace length. The facets across the cornea are quite different in shape and size; the most central facets are hexagonal in hexagonal packing (about 35 µm), while the peripheral facets towards the eyestalk are considerably smaller (around 14.5 µm) and with irregular shapes and packing (Fig. 6.7K, L; Table 6.1).

The genera in the subfamily Notopodinae all have well developed eyes on long eyestalks. In *Cosmonotus grayi*, the length of the podophthalmite seems to be the most extreme across raninoids, measuring half the length of the dorsal carapace (Fig. 8A). Its cornea is sub-cylindrical (Fig. 8B), longer than wide, approximately 5% the length of the carapace, and it bears small flattened hexagonal facets around 20 µm in diameter, with hexagonal packing, and with raised facet edges (Fig. 6.8C; Table 6.1). *Notopus dorsipes* (Fig. 8D) and *Ranilia muricata* (Fig. 8G) also have corneae that are longer than wide, sub-cylindrical, with a diameter about 3% the carapace length, and three times shorter than the eyestalk. Their facets are also hexagonal, well defined, and packed in a hexagonal array. The facet diameter in *N. dorsipes* is around 26.5 µm (Fig. 6.8E,F), and 32 µm in *R. muricata* (Fig. 6.8H,I; Table 6.1).

The subfamily Ranininae has only one living genus and species, *Ranina ranina*. It is the largest of all raninoids, reaching carapace length sizes over 15 cm (Luque, unpublished data). *Ranina* eyes are elongate, elliptical to sub-cylindrical (Fig. 6.8J, K). The eyestalk has a long podophthalmite twice as long as the cornea, and a long basophthalmite articulating at an angle. Its orbits are narrower than the eyes, but the long podophthalmite and basophthalmite articulate in such a way that allows the eye to be retracted semi-vertical into the orbit. The cornea diameter is on average 5% the carapace length, and is made up of thousands of hexagonal facets packed hexagonally with an approximate diameter of 52 µm (Fig. 6.8K,L; Table 6.1).

Finally, extant genera in the subfamily Raninoidinae share the presence of small elliptical eyes on longer eyestalks, all bearing hexagonal facets in hexagonal packing. All three taxa have sub-horizontal orbits with two well-developed orbital fissures and orbital spines. In the studied specimen of *Notopoides latus* (Fig. 6.9A) the cornea width is 5% the carapace length, and the facets measure around 42 µm (Fig. 6.9B, C), while in *Notosceles viaderi* (Fig. 6.9D) the cornea width is less than 3% the carapace length, and the facets measure around 38 µm (Fig. 6.9E, F; Table 6.1). The eyestalks of *Raninoides benedicti* (Fig. 6.9G) are longer than in the other Raninoidinae genera, approximately four times as long as the cornea. The cornea diameter is 2.5% the carapace length, and the facets measure 26 µm in diameter (Fig. 6.9H,I; Table 6.1).

6.3.2.5. Cyclodorippoidea

Little is known about the eyes in cyclodorippoid crabs overall. The specimen of *Clythrocerus nitidus* studied here (Fig. 6.9J) has small, roundish eyes, with a cornea nearly as long as wide, and as long as the podophthalmite. The cornea diameter is approximately 11% of carapace length, and is covered in small, well-defined hexagonal facets in hexagonal array. Facet diameter is 35 µm (Fig. 6.9K, L; Table 6.1). Previously, round facets in hexagonal packing have been reported for *Krangalangia spinosa* (see Scholtz and McLay, 2009), supporting the absence of mirror eyes in cyclodorippoid crabs.

6.3.2.6. Eye types in other fossil brachyuran crabs

One specimen of *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Raninoida: Necrocarcinoidea) from the lower Coniacian of Colombia (Upper Cretaceous, ~88 Mya) (Fig. 6.10A–C) exhibits the first recorded instance of preservation of compound eyes in fossil raninoidans. Specimen, 320018–022, possibly a female, is of small size (~1.6 cm carapace width), and preserved in ventral view (Fig. 6.10A). Its right eye is small, roundish in outline, and has a short eyestalk (Fig. 6.10B). The eye portion that is exposed bears small hexagonal facets packed in hexagonal arrangement (Fig. 6.10C). †Cenomanocarcinidae belongs to a group of ancient crab-like raninoidans (Necrocarcinoidea) distantly related to fossil frog-like groups such as †Palaeocorystoidea, from which Raninoidea likely evolved (van Bakel *et al.*, 2012a; Karasawa *et al.*, 2014; Luque, 2015a; Schweitzer *et al.*, 2016).

A fossil eubrachyuran indeterminate from the Santonian (Upper Cretaceous, 85 Mya) of Colombia (Fig. 6.10D–F), has large eyes bearing several small hexagonal facets packed in a hexagonal pattern. Likewise, a fossil freshwater crab from the Miocene of Panama (Neogene, ~16 Mya), has three-dimensional eyes bearing small hexagonal facets in hexagonal packing as seen across freshwater crabs (Fig. 6.10G–I).

6.4. Discussion

6.4.1. Interpretation of ommatidial packing and facet shape in podotreme crabs

Although external optical features alone cannot reveal details of eye light-path adaptations, they are useful for identifying the presence or absence of reflecting superposition eyes and their distinctive square facets in an orthogonal lattice. This is particularly useful when aiming to understand the fossil record of crustacean compound eyes, since only in a few exceptional cases are internal structures preserved (e.g., Vannier *et al.*, 2016). Eyes of the apposition, refracting superposition, and parabolic superposition types, have different internal structural mechanisms to focus the light beams into the retina and form images, but they share the hexagonal to roundish external shape of the facets packed in a hexagonal lattice. A hexagonal array is an efficient way to pack cylindrical or hexagonal ommatidia into an eye, reducing the angular separation of the ommatidia to a minimum and increasing the eye resolution (Gaten, 1998). Reflecting superposition eyes, however, have distinctive square facets in an orthogonal to rectilinear array indicating 'mirror' optics with underlying square crystalline cones.

In *Callichimaera*, hexagonal to round facets in hexagonal packing are the dominant feature throughout the cornea, suggesting of apposition, parabolic superposition, or less likely, refracting superposition eyes. One small specimen of *Callichimaera*, however, has some proximal sub-square facets with rectilinear packing near the contact with the eyestalk (Fig 4.3B–D). In decapod crustaceans, the presence of two types of facets in the same eye is uncommon, with only a handful of fossil and extant species showing a combination of hexagonal and square facets. For instance, the larval to early juvenile instars of the shrimp *Oplophorus spinosus* (Brullé, 1839), *Systellaspis debilis* (A Milne-Edwards, 1881a), and a post-larval vent shrimp likely of *Rimicaris exoculata* Williams and Rona, 1986, show a mosaic of hexagonal and square facets likely associated with the transition form the larval apposition to the post-larval reflecting superposition eye type (Gaten and Herring, 1995; Gaten *et al.*, 1998). Likewise, a fossil polychelidan lobster specimen from the Jurassic of France (Audo et al. in progress) has two facet shapes in the same eye, but whether they represent a true regionalization of the eye or an artifact of the packing is unclear. The presence of squarish facets in one specimen of †*Callichimaera* thus may be the result of local facet packing rather than a true regionalization or transition between eye types.

Raninoids or "frog" crabs are one of the main brachyuran groups for which visual systems are largely unknown, in part due to their cryptic lifestyle and range of bathymetric depths (from 5 to 1000 m depth) (Tucker, 1995; Luque, 2015a) making their collection and study difficult. Extant raninoids are adapted for burrowing in sand or soft sediment (Bourne, 1922; Števčić, 1973; Tucker, 1998; Luque, 2015a). Their particular 'frog-like' morphology with elongated carapace, a pleon that is partially exposed dorsally, elongated mouthparts, modified sternites, naked pleura, and modified distal podomeres of their walking legs, are regarded as adaptations for their burrowing habit (see Chapter 3). Gaten (1998) suggested that the relatively small eyes in *Ranina* are also an adaptation to a fossorial lifestyle. Extant raninids remain buried in the substratum during the day, emerging at night to search for food (Skinner and Hill, 1986). Some taxa like *Ranilia, Ranina*, and particularly *Cosmonotus*, have relatively large eyes covered in small facets of nearly the same size throughout the cornea, and have long podophthalmite eyestalks that can be held outside the sediment when buried (Fig. 6.8). Conversely, raninid crabs like *Symethis* (Fig. 6.7J) show an extreme reduction of the eye and eyestalk, with the cornea enclosed in a reduced orbit and bearing only a couple of hundred facets with different shapes, sizes, and packing (Fig. 6.7K,L). *Symethis* eyes seem to be degenerate and with poor resolving power.

Since frog crabs occupy an intermediate position between the earliest brachyuran branches (i.e., Homolodromioidea, Dromioidea, Homoloidea), and the more derived groups (i.e., Cyclodorippoidea and Eubrachyura), understanding raninoid optics is pivotal to testing hypotheses of visual system distributions across brachyurans and their phylogenetic significance. The clear hexagonal facets in hexagonal packing in the lyreidids *Lyreidus* and *Lysirude*, and the raninids *Cosmonotu*s, *Cyrtorhina*, *Symethi*s, *Notopus*, *Ranilia*, *Ranina*, *Notopoides*, *Notosceles*, and *Raninoides*, strongly indicate the absence of reflecting superposition in this group, contradicting the assumption by Gaten (1998) (see also table 1 in Porter and Cronin, 2009) that raninoids likely have mirror eyes as basal podotremes Dromioidea, Homolodromioidea, and Homoloideans do. My findings indicate that the visual systems present in raninoideans are of the apposition or parabolic superposition type, thus more similar to the visual systems in eubrachyurans than in more distant podotremes (Figs 6.7–9, 6.11). Furthermore, the fossil *Cenomanocarcinus* from Colombia preserves an eye bearing small hexagonal facets packed in hexagonal arrangement, which suggests that the loss of mirror optics in adult total group stem and crown raninoidans must have occurred in a recent common ancestor of Necrocarcinoidea, Palaeocorystoidea, and Raninoidea more than 80 Mya.

Cyclodorippids are crabs mostly found in deeper waters, and the eyes of some species might be degenerative. The cyclodorippoid crab studied here conforms to the absence of mirror eyes with square facets seen in more basal podotremes.

The eyes of Homolodromioidea, Dromiodea, and Homoloidea all share the plesiomorphic presence of adult eyes with square facets packed in an orthogonal lattice typical of reflecting superposition optics. Square facets are essential to the mirror mechanisms (Fincham, 1980; Vogt, 1980, and their presence in the less inclusive brachyuran clades contrasts with the lack of reflecting superposition eyes in other brachyurans.

6.4.2. The eye of the chimaera

Most decarcinized groups of false and true crabs are fossorial and have reduced eyes on long eyestalks that the animals can keep outside the sediment while buried. In *Callichimaera*, however, the large eyes with very short eyestalks differ drastically from the eyes of similar looking crabs (see Chapter 4, Figure 4.4). Furthermore, †*Callichimaera* lacks any associated protective structures such as orbits or orbital spines (Figs 6.3, 6.4), indicating that its eyes must have remained exposed at all times even under times of stress. Such eyes and lack of orbits are mostly seen in crab megalopae, before they metamorphose into their post-larval stage. *Callichimaera*'s large and unprotected globular eyes and its overall body form have been interpreted as possible paedomorphic retention of larval traits retained in adulthood (Chapter 4). Active burrowing/swimming behaviour is inferred based on the functional morphology of its dorsally and ventrally keeled carapace, and large, flattened paddle–like pereiopods 2 and 3.

In terms of overall size and orbital construction, the eyes of †*Callichimaera* are more similar to those *Ekalakia exophthalmos* Feldmann *et al.*, 2008b; a dromiacean crab from the Campanian–Maastrichtian (70 Mya) Pierre Shale Formation in the USA. In both taxa, the eyes are very large relative to the body, have short eyestalks, and exhibit a limited development of protective structures for the eye (Feldmann *et al.*, 2008b). The material of *Ekalakia*, however, does not preserve corneal cuticle bearing facets.

6.4.3. Eye preservation in fossil crabs

Aside from †*Callichimaera perplexa* (Figs 6.3–6.4), facet-bearing fossil eyes have been found in the extinct etyoid *Caloxanthus americanus* Rathbun, 1935b, from the Cenomanian of Texas (Vega *et al.*, 2014), and in the three Cretaceous and Neogene crabs here reported (Fig. 6.10). Although preservation of crabs eyes is rather unusual (Klompmaker *et al.*, 2017), I show that external and internal visual elements in fossil brachyurans do occur in a number of taxa from different groups, lithologies, and ages. Miocene crabs preserved in amber from Mexico (Serrano-Sánchez *et al.*, 2016) likely have hexagonal facets of apposition / parabolic superposition eyes. Tanaka *et al.* (2009) reported isolated decapod eyes bearing hexagonal facets from the Aptian–Albian Romualdo Formation of Brazil (115–110 Mya), presumably from a phyllosoma larva. Also from the Romualdo Formation are some fossil crab zoeae preserved as stomach content in the fish *Tharrhias* ((Maisey and Carvalho, 1995; Luque, 2015a; see Chapter 3). Hexagonal facets in hexagonal packing as seen in extant crab zoeae.

6.4.4. Phylogenetic implications

The apposition eye is the simplest eye type and is present in all decapod larvae. Larval apposition eyes in decapod crustaceans are pre-adapted to be of the superposition type by migrating the eye pigments to avoid predation, and thus resulting in a ‘clear zone’ between the cones and the rhabdom, and functioning as a facultative superposition eye (Gaten, 1998).

Although decapod larvae have apposition eyes, adult decapods of most shrimp, lobster, galatheoid anomuran, and ancient brachyuran clades share a unique reflecting superposition visual system not seen in other crustaceans outside Decapoda (Land, 1976; Scholtz and McLay, 2009; Tudge et al., 2012; Gaten et al., 2013). Noticeably, many decapod lineages have independently retained larval apposition eyes (Gaten, 1998; Cronin and Porter, 2008; Porter and Cronin, 2009); or have evolved refractive or parabolic superposition eyes while retaining hexagonal facet shape and packing (Nilsson, 1988). Apposition and reflecting superposition eyes are more or less homogeneous across taxa, while the mechanisms in the parabolic and refracting superposition are more variable and with intermediate forms (Nilsson, 1983; Nilsson, 1990a; Porter and Cronin, 2009).

Reflecting superposition eyes likely evolved only once in a recent common ancestor of Decapoda during the Paleozoic, possibly related to deep-water habitat or nocturnal behaviour. Among brachyurans, mirror optics are found in the least inclusive brachyuran lineages (early lineages) Homolodromioidea, Dromioidea, and Homoloidea, and are absent in more derived podotreme brachyurans like Raninoidea and Cyclodorippoidea, and the most inclusive and diverse of all crabs, the Eubrachyura (Fig 6.11). We should keep in mind, however, that ecology plays a crucial role in shaping the visual systems an organism to better suit their biology, and a number of taxa with a given eye type are likely to undergo adaptations to better suit their current ecological pressures.

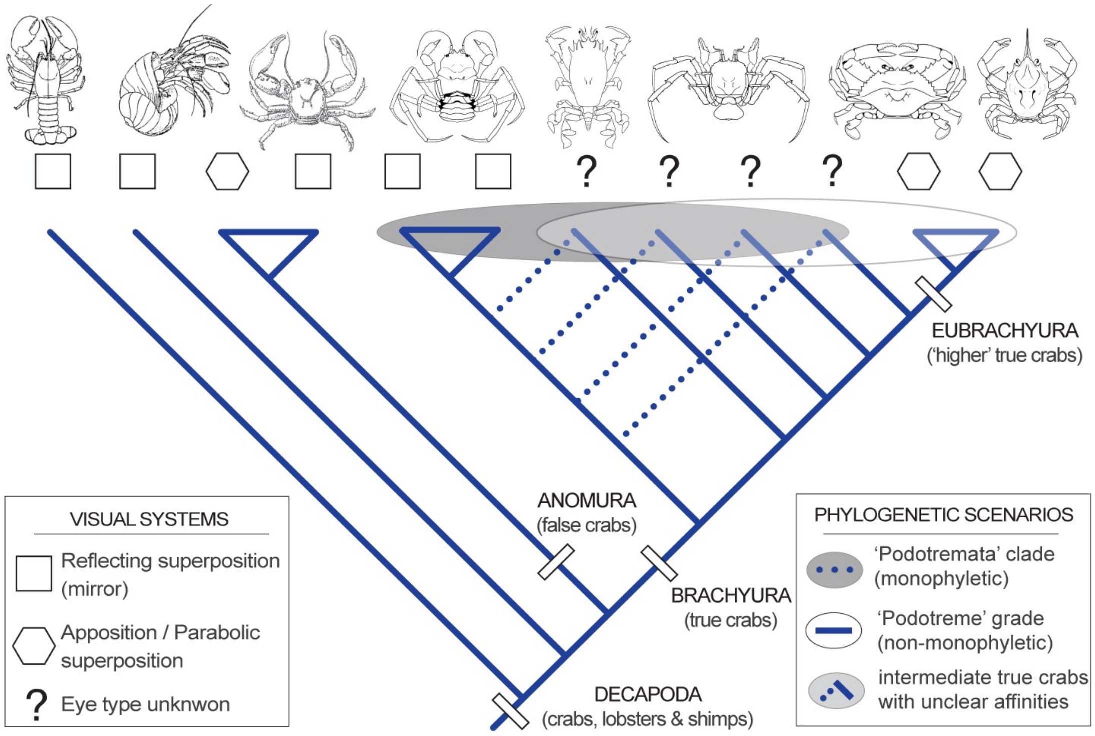


Figure 6.1. Phylogenetic scenarios for the evolution of true crabs, and the distribution of their visual systems. The main competing hypotheses suggest that either 'lower' true crabs, or podotremes, form a monophyletic clade Podotremata (dark grey oval, dotted lines), whereas podotreme crabs may represent a paraphyletic grade of increasing complexity (white oval, solid lines) with some intermediate groups closer to eubrachyurans than to other podotremes (intersect light grey oval). While 'lower' brachyurans share mirror optics (white squares), the 'higher' brachyurans lack mirror eyes altogether and have only apposition/parabolic superposition eye types (white hexagons). The visual systems in intermediate 'lower' podotremes (marked with '**?**'), as well as the origins of their carcinized and decarcinized body plans (light grey oval intersect), are still unresolved.

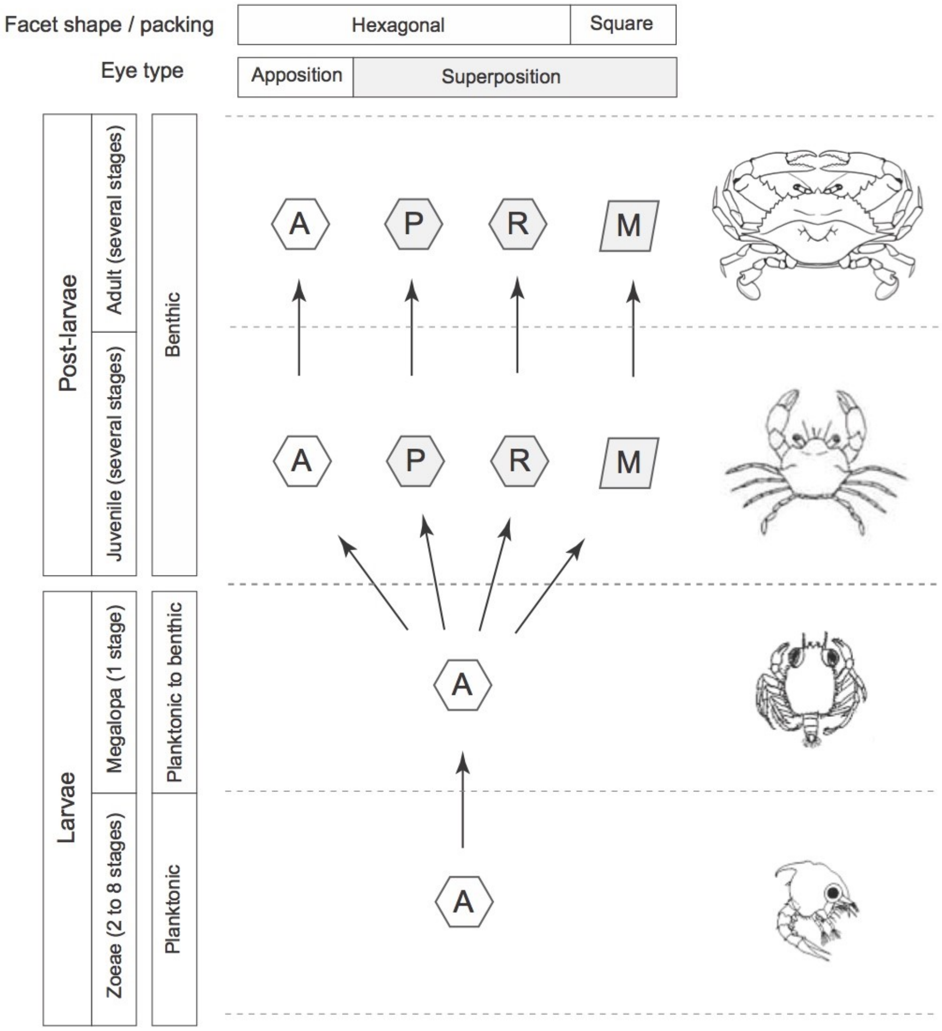


Figure 6.2. Distribution of eye types in crabs across life stages. In larval stages, brachyurans and other decapod crustaceans have apposition eyes, which is the ancestral state for malacostracans. In post-larval stages, the larval apposition eyes might either remain functional as apposition eyes, or undergo internal and external restructuration to function as superposition eyes. Externally, apposition (A), parabolic superposition (P), and refracting superposition (R) eyes share the hexagonal packing of hexagonal to round facets, while eyes of the reflecting superposition type (M) are modified to work as a mirror box, and have square facets with orthogonal packing.

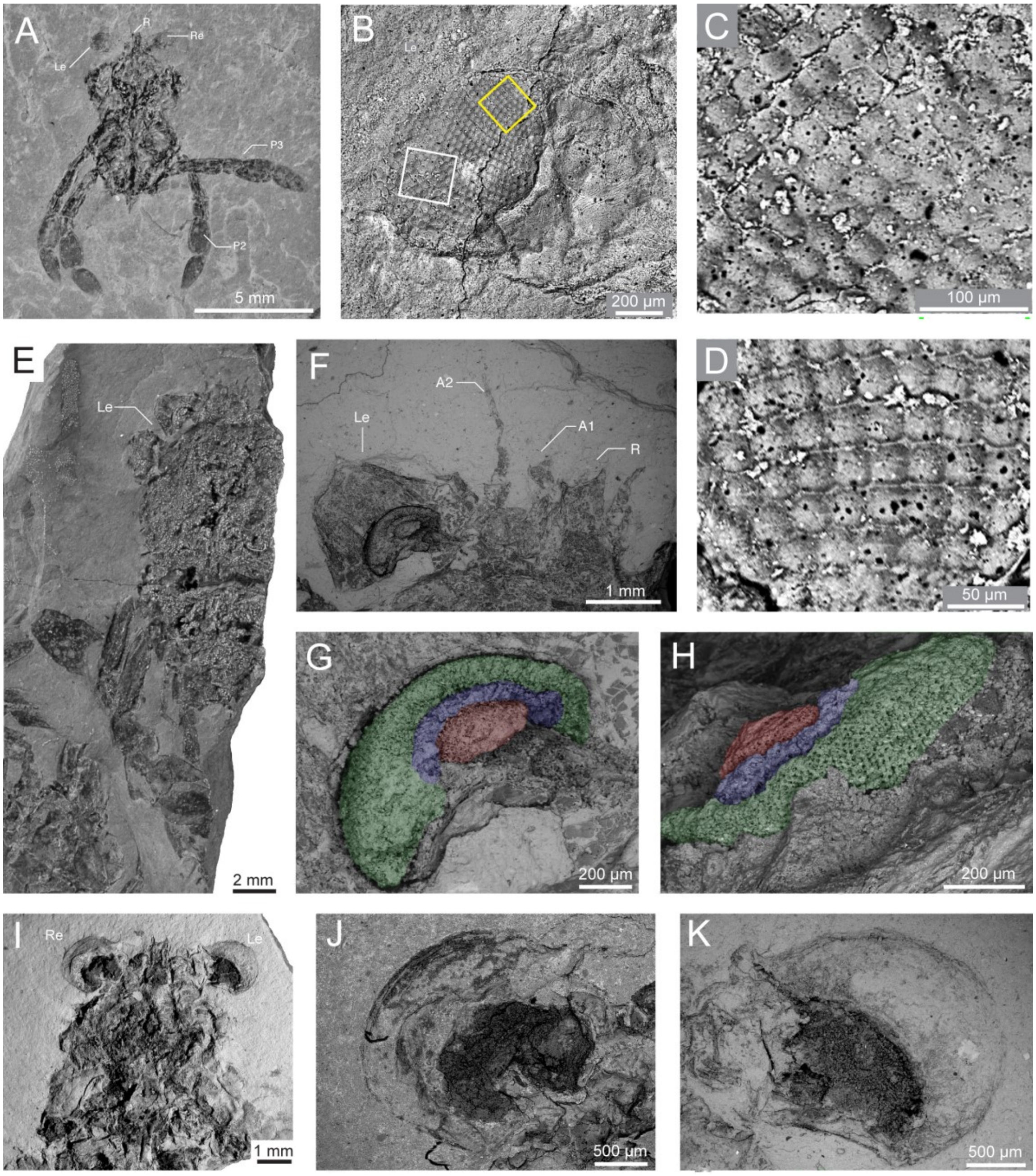


Figure 6.3. Specimens of †*Callichimaera perplexa* with eyes preserved. A–D: Paratype IGM p881220; A, specimen in ventral view with eyes and legs P2–P3; B, left eye bearing hexagonal facets in hexagonal array (white box) (C), and a region of the eye with squarish facets in rectilinear array (yellow box) (D). E–H: Paratype IGM p881209a, dorsal view; E, specimen preserving internal remains, antennae, and the left compound eye; F, close–up of anterior portion showing the first and second antenna the left eye, and the rostrum; G, dorsal view of left eye showing three retinal layers in the optical lobe; H, oblique view of retinal layers. I–K: Paratype IGM p881208, ventral view; I, specimen showing large eyes and rostrum bifid; J, close–up of left eye; K, close–up of right eye. Abbreviations: A1: first antenna (antennula); A2: second antenna (antenna s.s.); Le–Re: left and right eyes; P2–P3: pereiopods 2 to 3; R: rostrum. A and E coated with ammonium chloride; B–D, F–H, J–K dry and uncoated SEM images

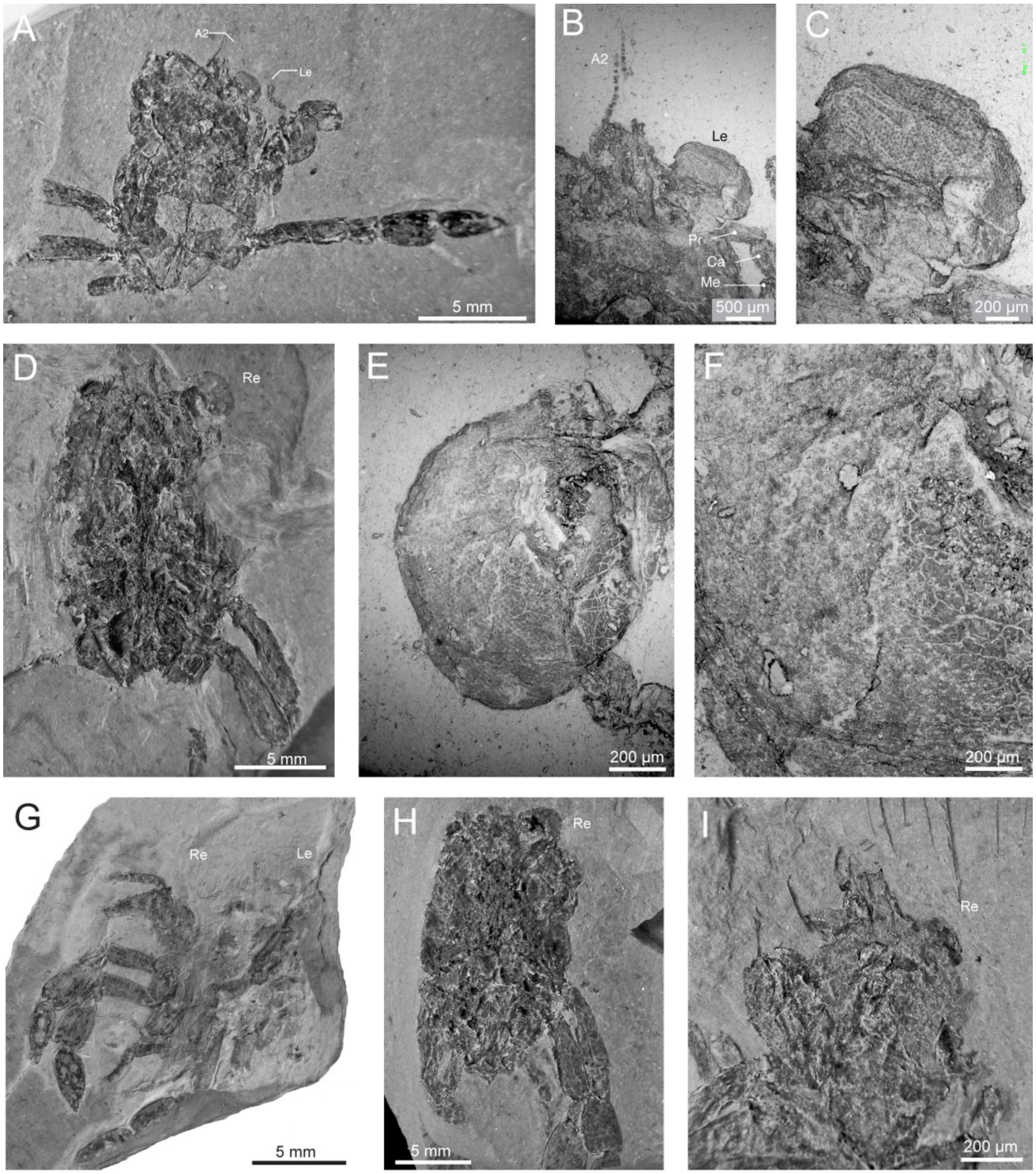


Figure 6.4. Specimens of †*Callichimaera perplexa* with eyes preserved (cont.). Specimens coated with ammonium chloride, except for SEM images. A–C, Paratype IGM p881210, ventral view; A, specimen showing the second antennae and left compound eye; B, SEM of anterior portion, showing the mxp3, antennae, and left compound eye; C, SEM image showing details of the facets. D–F: Paratype IGM p881207; D, specimen showing legs P2–P3, and right eye; E, SEM image of right eye; F, SEM close–up of the same eye, showing facets in hexagonal arrangement. G, Paratype IGM p881219, ventral view showing the chelipeds, legs P2–P5, both eyes, and rostrum. H, Paratype IGM p881211, showing right eye. I, Paratype IGM p881192, showing a preserved eye. Abbreviations: A2: second antenna (antenna s.s.); Ca: carpus; Le–Re: left and right eyes; Me: merus; Pr: propodus. A, D, G–I coated with ammonium chloride; B–C, E–F, dry and uncoated SEM images.

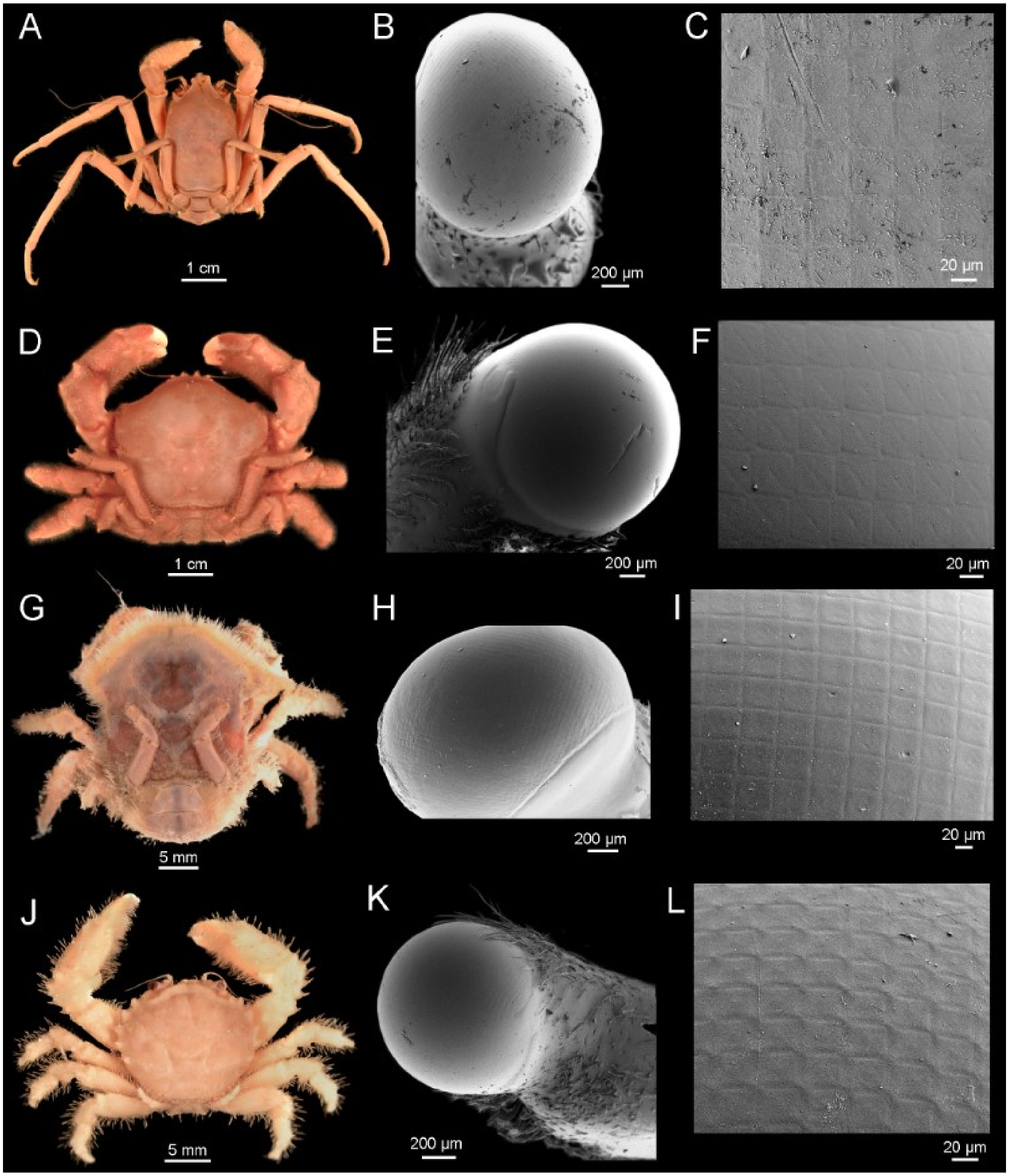


Figure 6.5. Homolodromioidea and Dromioidea. A–C, Homolodromioidea: Homolodromiidae: *Dicranodromia felderi* Martin, 1990, USNM 252207; A, dorsal view of female; B, SEM image of right eye; C, details of the cornea bearing square facets in orthogonal packing. D–I, Dromioidea: Dromiidae; D, ?*Moreiradromia sarraburei*, USNM 1277453, dorsal view of male; E–F, *Dromia personata* (Linnaeus, 1758), USNM 1277452, female; F, SEM image of right eye; F, details of the cornea bearing square facets in orthogonal packing; G–I, *Hypoconcha* sp., 186466; G, dorsal view of male; H, SEM image of right eye; I, details of the cornea bearing square facets in orthogonal packing. J–L, Dromioidea: Dynomenidae: *Dynomene filholi* Bouvier, 1894, USNM 121402; J, dorsal view of male; K, SEM image of right eye; L, details of the cornea bearing square facets in orthogonal packing.

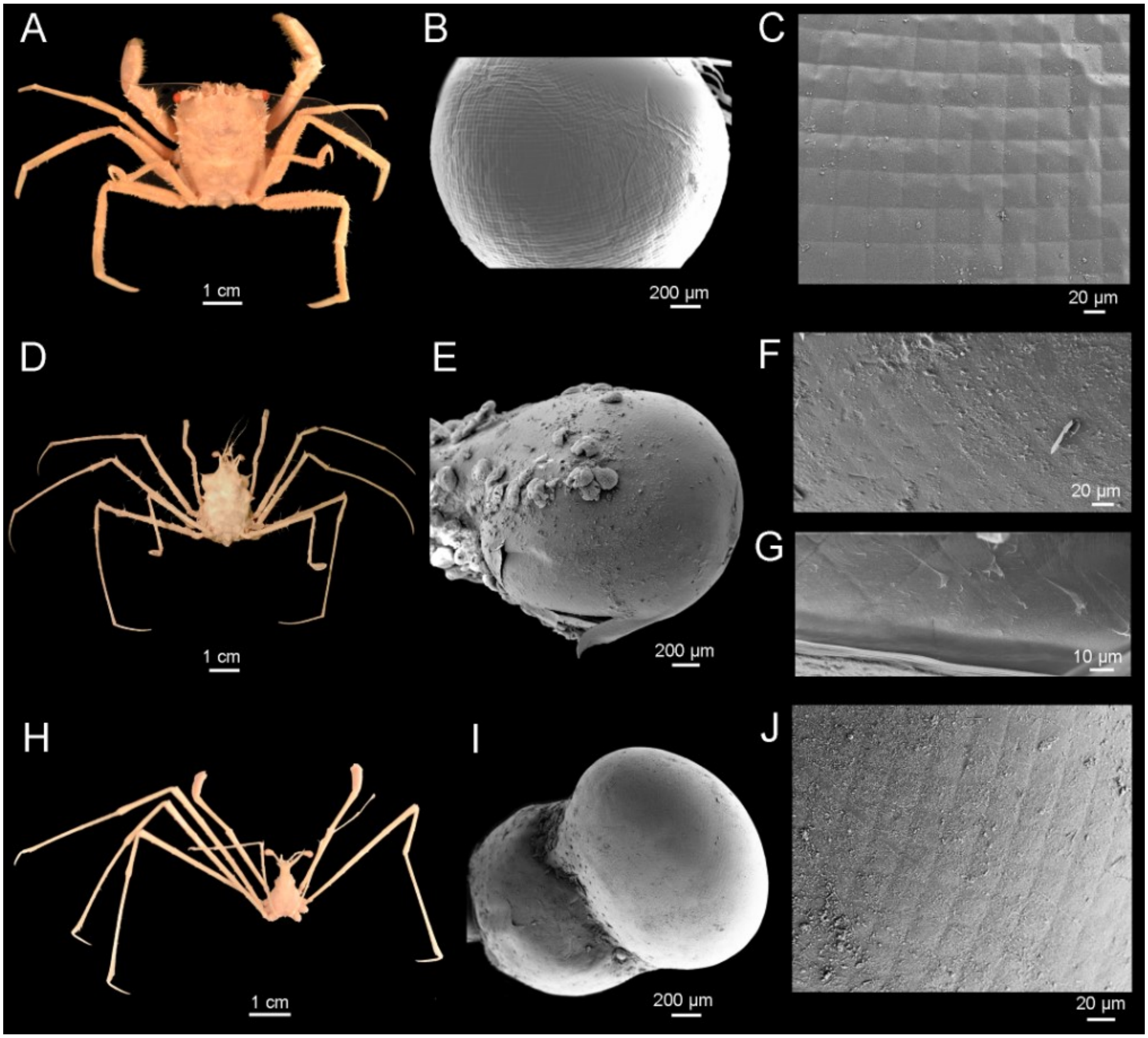


Figure 6.6. Homoloidea. A–G, Homolidae; A–C, *Homola minima* Guinot and Richer de Forges, 1995, USNM 1185786; A, dorsal view of male; B, SEM image of globular right eye; C, details of the cornea bearing square facets in orthogonal packing. D–F, *Latreillopsis bispinosa* Henderson, 1888, QMW.17070; D, dorsal view; E, SEM image of right eye; F, details of the cornea bearing square facets in orthogonal packing; G, detail of the eye under the cuticle, showing square facets in orthogonal packing. H–I, Latreillidae: *Eplumula phalangium* (De Haan, 1839), USNM 74587; H, dorsal view of male; I, SEM image of right eye and podophthalmite; J, details of the cornea bearing square facets in orthogonal packing.

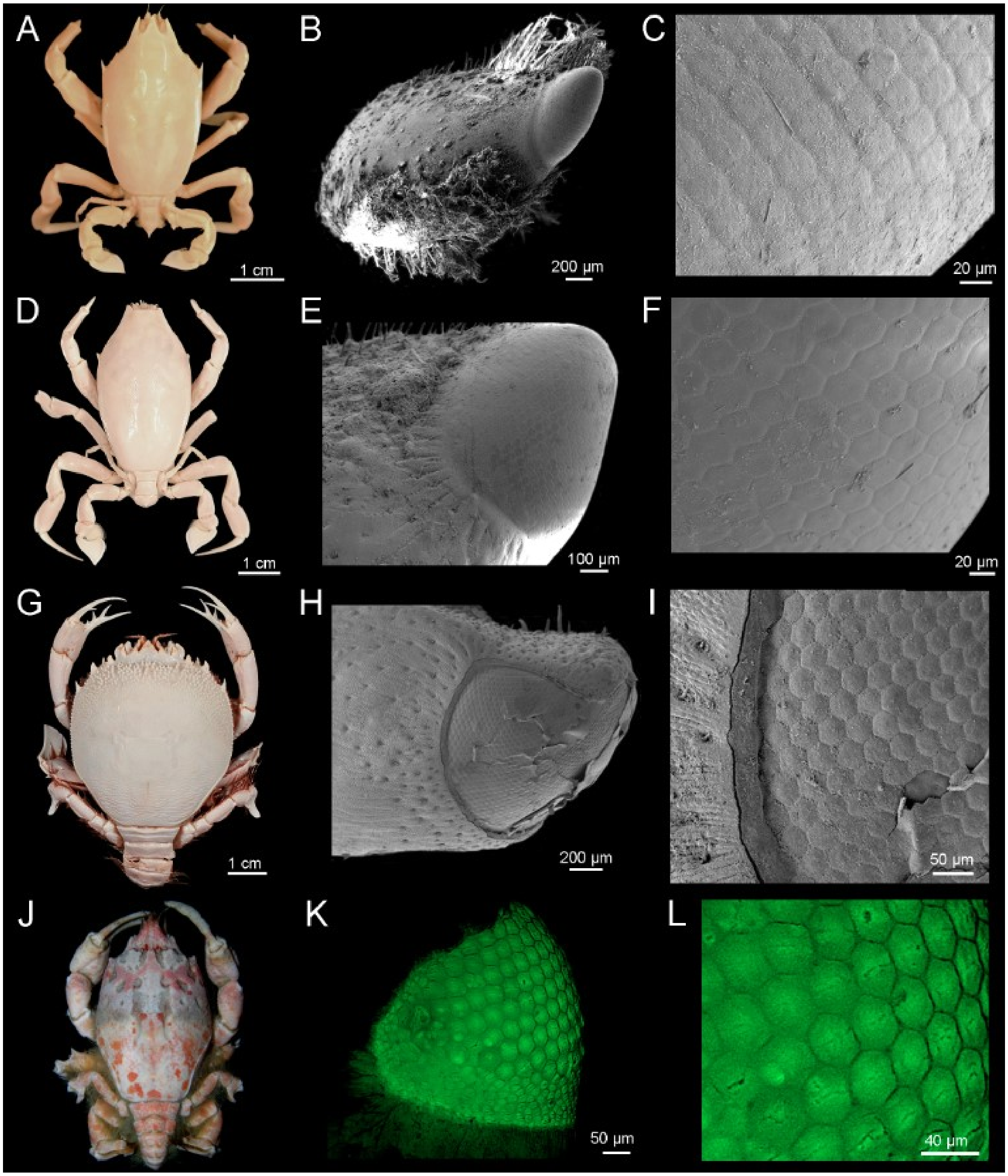


Figure 6.7. Raninoidea: A–F, Lyreidididae; A–C, *Lysirude nitidus* (A. Milne-Edwards, 1880a) (=*Lyreidus bairdii*), USNM 66638; A, dorsal view of female; B, SEM image of small right eye in a stout podophthalmite; C, details of the cornea bearing hexagonal facets in hexagonal packing. D–F, *Lysirude griffini* Goeke, 1985, USNM 216726; D, dorsal view of male; E, SEM image of small right eye; C, details of the cornea bearing hexagonal facets in hexagonal packing. G–I, Raninidae: Cyrtorhininae: *Cyrtorhina granulosa* Monod, 1956, MNHN-IU-2016-2020 (= MNHN-B16181); G, dorsal view of female; H, SEM image of small right eye; I, details of the cornea bearing hexagonal facets in hexagonal packing. J–L, Raninidae: Symethinae: *Symethis* sp., uncatalogued specimen; J, dorsal view of male; K, Confocal microscope image of small right eye showing the different shapes and sizes of facets through the cornea; L, details of the cornea bearing hexagonal facets in hexagonal packing.

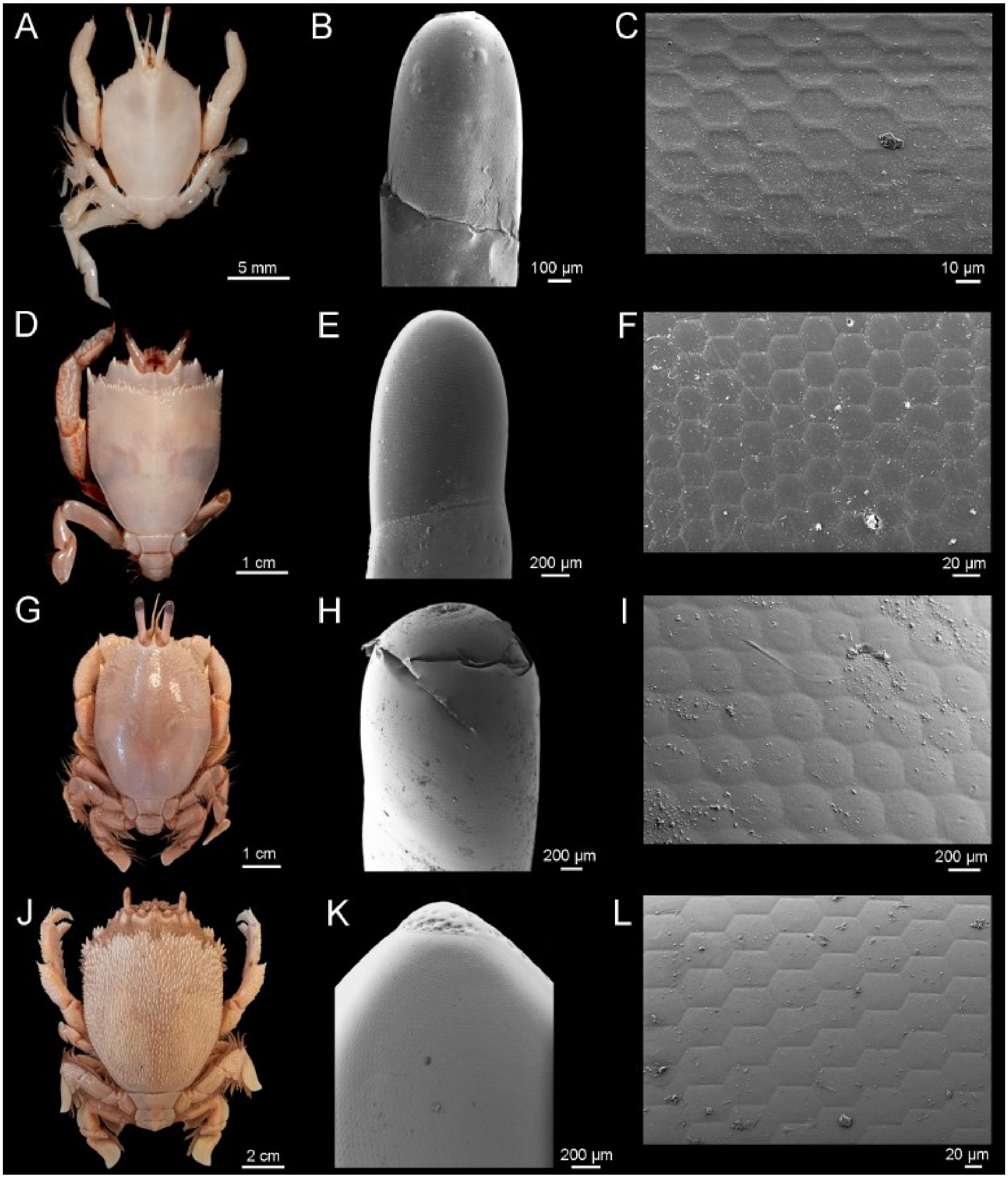


Figure 6.8. Raninoidea (cont.): A–I, Raninidae: Notopodinae; A–C, *Cosmonotus grayi* White, 1848, MNHN-IU-2016-2024; A, dorsal view of male; B, SEM image of right eye; C, details of the cornea bearing hexagonal facets in hexagonal packing. D–F, *Notopus dorsipes* (Linnaeus, 1758), MNHN-IU-2016-2023 (= MNHN-B7933); D, dorsal view of male; E, SEM image of left eye; F, details of the cornea bearing hexagonal facets in hexagonal packing. G–I, *Ranilia muricata* H. Milne Edwards, 1837, USNM 121656; G, dorsal view of female; H, SEM image of right eye; I, details of the cornea bearing hexagonal to circular facets in hexagonal packing. J–L, Raninidae: Ranininae: *Ranina ranina* (Linnaeus, 1758), J, dorsal view of specimen USNM 239219; K–L, specimen USNM 265062, female; K, SEM image of right eye; L, details of the cornea bearing hexagonal facets in hexagonal packing.

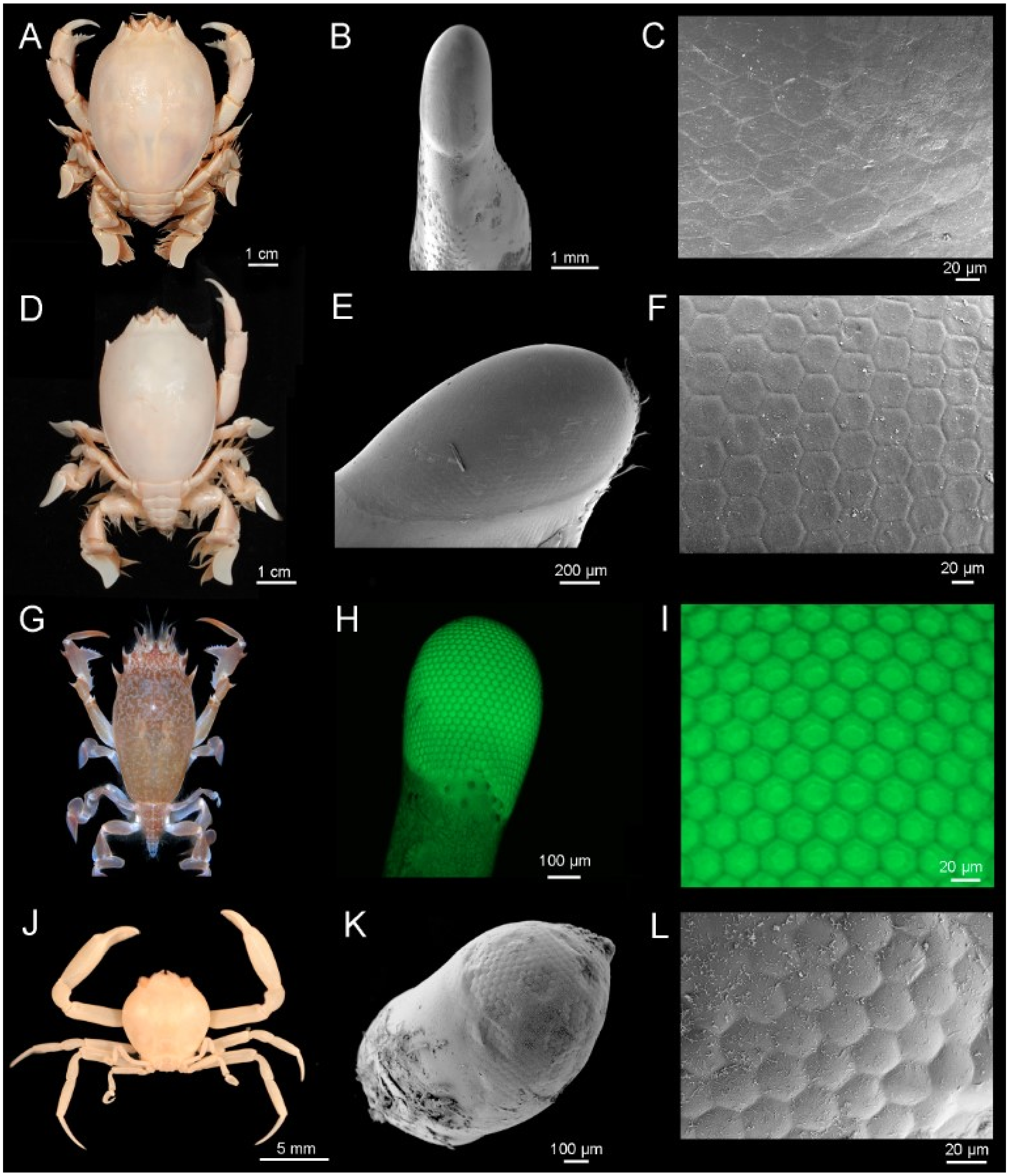


Figure 6.9. Raninoidea and Cyclodorippoidea. A–I, Raninoidea: Raninidae: Raninoidinae: A–C, *Notopoides latus* Henderson, 1888, MNHN-IU-2016-2025 (= MNHN-B19110); A, dorsal view of male; B, SEM image of right eye and eyestalk; C, details of the cornea bearing hexagonal facets in hexagonal packing. D–F, *Notosceles viaderi* Ward, 1942, MNHN-IU-2016-2029 (= MNHN-B28964); D, dorsal view of male; E, SEM image of right eye; F, details of the cornea bearing hexagonal facets in hexagonal packing. G–I, *Raninoides benedicti* Rathbun, 1935a, specimen uncatalogued; G, dorsal view of male; H, Confocal miscroscope image of right eye and eyestalk; I, close up of the cornea bearing hexagonal facets in hexagonal packing. J–L, Cyclodorippoidea: Cyclodorippidae: *Clythrocerus nitidus* (A. Milne-Edwards, 1880a), USNM 77380; J, dorsal view of male; B, SEM image of small right eye; C, details of the cornea bearing hexagonal facets in hexagonal packing. Photo G courtesy of Arthur Anker.

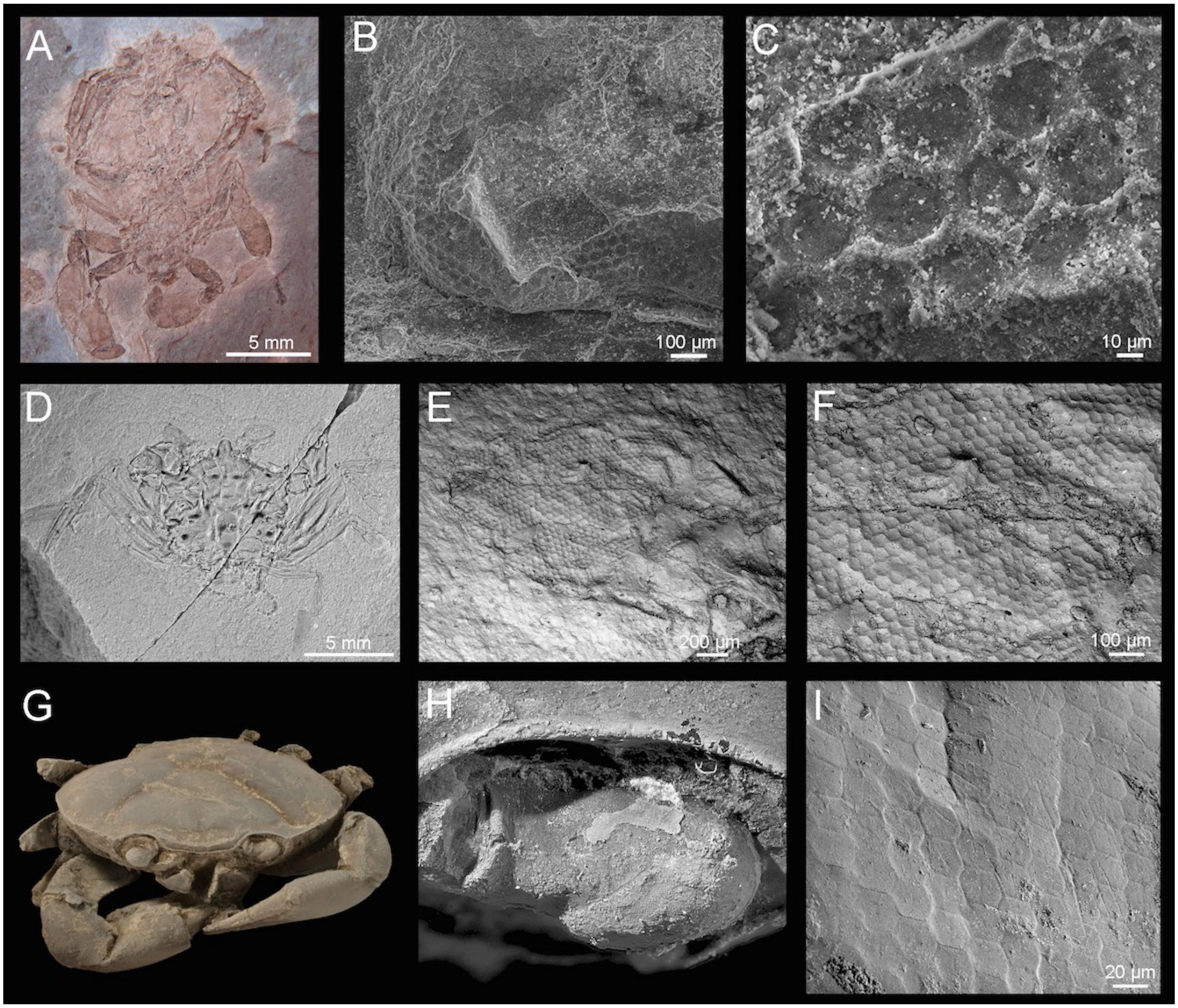


Figure 6.10. Other fossil brachyuran crabs preserving compound eyes. A–C: †Necrocarcinoidea: †Cenomanocarcinidae: †*Cenomanocarcinus vanstraeleni* Stenzel, 1945, specimen 320018–022, Coniacian of Boyacá, Colombia; A, ventral view of female; B, SEM image of the anterior portion, showing the right eye (Re); C, close-up showing small hexagonal facets in hexagonal packing. D–I, Eubrachyura; D–F, eubrachyuran indet., Santonian of Boyacá, Colombia; D, negative of male dorsal carapace showing the pereiopods, pleon, chelipeds, and large compound eyes; E, SEM image of compound eye bearing facets; F, close-up showing small hexagonal facets in hexagonal packing. G–I, Pseudothelphusoidea: Pseudothelphusidae indet., uncatalogued specimen, Miocene of Panama, Panama; G, frontal view showing the fronto-orbital region, the 3rd maxillipeds, and the compound eyes; H, close-up of the left eye; I, details of the cornea preserving hexagonal facets in hexagonal packing. Dagger (†) indicates extinct taxa.

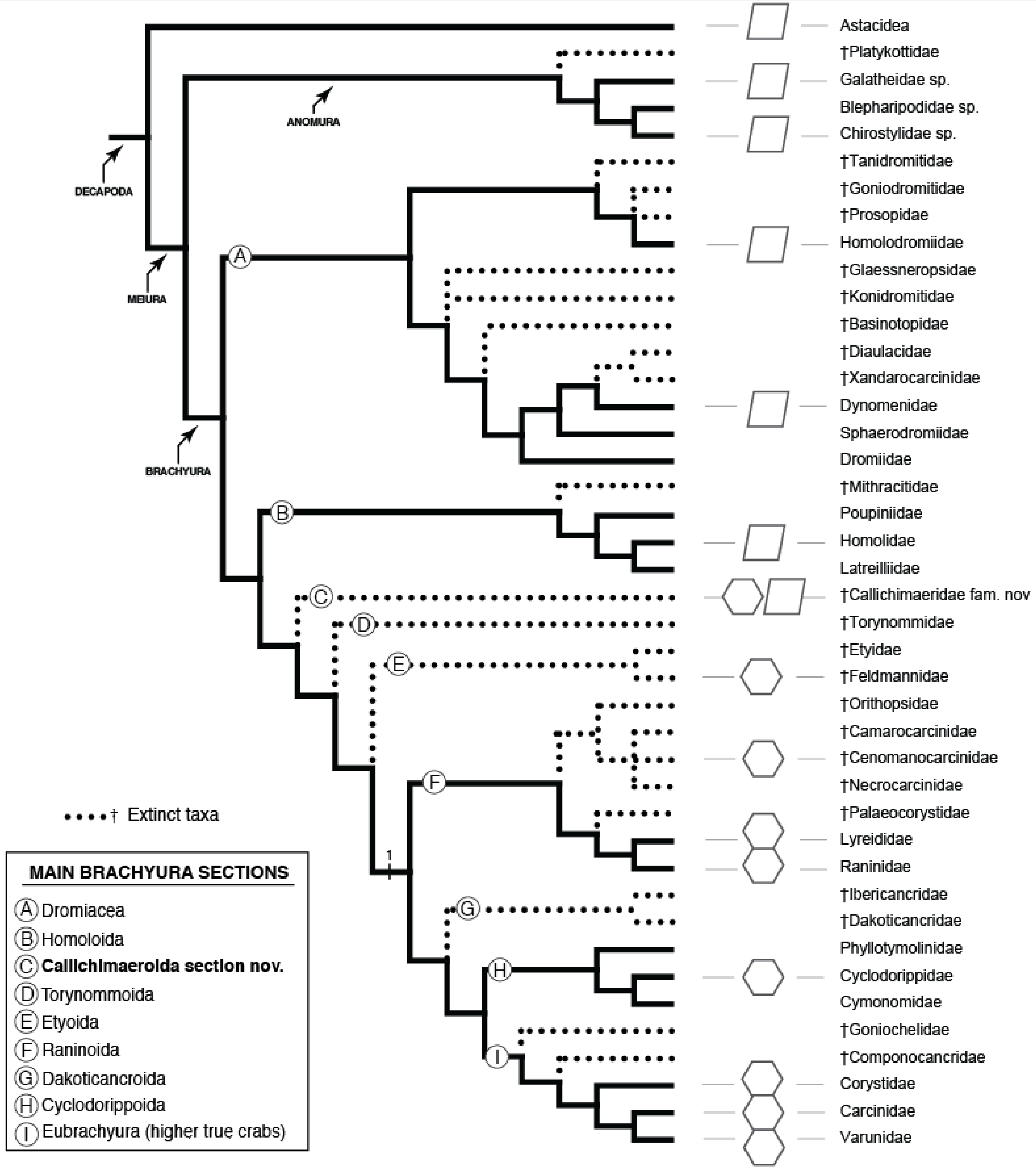


Figure 6.11. Distribution of visual systems in Brachyura. Hexagons: hexagonal facets with hexagonal packing, typical of apposition, parabolic superposition, and refracting superposition eyes. Squares: square facets in an orthogonal array typical of reflecting superposition eyes, or ‘mirror’ eyes.

Table 6.1. List of extant podotreme and fossil brachyuran specimen studied bearing compound eyes. Abbreviations: CL: carapace maximum length; CorL: cornea length; CorW: cornea width/diameter; Cw: carapace maximum width; FD: facet diameter; mm: millimeters; µm: microns.

Collection ID	Taxon	Locality	Facet shape / array	CorW (mm)	CorL (mm)	CL (mm)	CW (mm)	CorW / CL	FD (µm)
USNM 252207	Homolodromiidae: *Dicranodromia felderi*	North Atlantic Ocean, Caribbean Sea (see in Martin, 1990)	Square / orthogonal	1.53	1.50	23.00	17.70	6.65	35.00
USNM 1277452	Dromiidae: *Dromia personata*	Indet	Square / orthogonal	1.66	1.56	28.60	34.00	5.80	35.77
USNM 186466	Dromiidae: *Hypoconcha* sp.	North Atlantic Ocean, United States	Square / orthogonal	1.66	1.15	17.90	18.80	9.27	39.90
USNM 121402	Dynomenidae: *Dynomene filholi*	West Africa, Annobion Island	Square / orthogonal	1.00	1.00	12.30	15.60	8.13	29.90
USNM 1185786	Homolidae: *Homola minima*	North Atlantic Ocean, Suriname, Northeast of Paramaribo	Square / orthogonal	2.00	2.00	27.40	24.40	7.30	30.60
QMW.17070	Latreillidae: *Latreillopsis bispinosa*	Off Tully Heads, NE Queensland	Square / orthogonal	1.80	1.90	23.40	16.50	7.69	35.00
USNM 74587	Latreillidae: *Eplumula phalangium*	Off Honshun Island, Japan	Square / orthogonal	1.52	1.18	11.50	6.80	13.22	24.50
IGM p881192	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.						
IGM p881207	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	2.70		17.00	8.60	15.88	
IGM p881208	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	1.90	1.70				
IGM p881209a	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	2.00		12.53		15.96	
IGM p881210	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	1.35		10.70	6.50	12.62	
IGM p881211	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	2.70		16.20	9.80	16.67	
IGM p881219	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Indet.	1.50	1.50				
IGM p881220	Callichimaeridae: *Callichimaera perplexa*	Cenomanian-Turonian Churuvita Group, Boyacá, Colombia	Hexagonal to squarish / hexagonal to orthogonal	0.81	0.70	6.60	3.80	12.27	33.10
320018-022	Cenomanocarcinidae: *Cenomanocarcinus* sp.	Coniacian Conejo Formation, Boyacá, Colombia	Hexagonal / hexagonal	0.75	0.75				35.00

Collection ID	Taxon	Locality	Facet shape / array	CorW (mm)	CorL (mm)	CL (mm)	CW (mm)	CorW / CL	FD (µm)
USNM 66638	Lyreididae: *Lysirude nitidus (Lyreidus bairdii)*	Isla Tortugas, Station #25. About 16 min South of #2 Red Buoy	Hexagonal / hexagonal	0.40	0.76	33.00	18.45	1.21	23.00
USNM 216726	Lyreididae: *Lysirude griffini*	North Pacific Ocean; United States; California, San Francisco Bay	Hexagonal / hexagonal	0.60	0.70	39.00	22.70	1.54	32.80
MNHN-IU-2016-2020 (= MNHN-B16181)	Raninidae: *Cyrtorhina granulosa*	Golfe de Guinée, I. Principe	Hexagonal / hexagonal	0.90	1.00	48.10	41.70	1.87	35.00
Uncataloged	Raninidae: *Symethis sp.*	Las Perlas, Panamá	Hexagonal / hexagonal	0.40	0.38	28.70	18.00	1.38	35.00
MNHN-IU-2016-2024	Raninidae: *Cosmonotus grayi*	Nouvelle Caledonie, Lagon Nord	Hexagonal / hexagonal	0.47	0.90	9.35	7.90	5.03	20.00
MNHN-IU-2016-2023 (= MNHN-B7933)	Raninidae: *Notopus dorsipes*	Musée de Manille, Philippines	Hexagonal / hexagonal	0.97	1.44	31.50	25.70	3.08	26.50
USNM 121656	Raninidae: *Ranilia muricata*	Florida, East Coast Near Fort Pierce	Hexagonal / hexagonal	1.69	2.50	40.20	30.10	4.20	32.00
USNM 265062	Raninidae: *Ranina ranina*	Taiwan, Tou Cheng Li Lan	Hexagonal	3.41	5.6	68.5	56	4.97	52.00
MNHN-IU-2016-2025 (= MNHN-B19110)	Raninidae: *Notopoides latus*	Iles Seychelles	Hexagonal / hexagonal	1.50	2.84	56.00	42.00	2.68	41.60
MNHN-IU-2016-2029 (= MNHN-B28964)	Raninidae: *Notosceles viaderi*	French Polynesia	Hexagonal / hexagonal	0.80	1.50	43.20	29.90	1.85	38.60
Uncataloged	Raninidae: *Raninoides benedicti*	Las Perlas Archipielago, Panama	Hexagonal / hexagonal	0.50	0.40				26.00
USNM 77380	*Clythrocerus nitidus*	Florida, Poustales Plateau	Hexagonal / hexagonal	0.66	0.66	5.90	6.50	11.19	35.00
320013-003	Eubrachyuran indet.	Mid Santonian Conejo Formation, Boyacá, Colombia	Hexagonal / hexagonal	1.29	1.28	6.80	7.00	18.97	40.90

Chapter 7. Conclusions and prospects

7.1. The fossil record of true crabs in the tropics

The findings presented in the preceding chapters, together with the re-examination of previous findings, new occurrences, and the revised systematic placement for several problematic or misidentified records, indicate that the fossil record of decapod crustaceans in tropical America is noticeably more diverse than previously envisioned, with a considerable endemism at the genus- and species-levels (Luque *et al.*, 2017b). This endemism is particularly marked in early stem raninoidans such as the †Orithopsidae, which are first known from the Aptian–Albian (Luque, 2014; Karasawa *et al.*, 2014; Schweitzer *et al.*, 2016). Five out of eight of these genera from the Early Cretaceous are endemic to northern South America (Luque *et al.*, 2017b; Prado *et al.*, submitted) (Chapter 5). The discovery of these new fossil raninoidans from the Early Cretaceous of northern South America, combined with recent phylogenetic analyses of fossil and extant necrocarcinoid, palaeocorystoid, and raninoid genera (Karasawa *et al.*, 2014; Luque, 2015a; Schweitzer *et al.*, 2016), support the hypothesis that a more 'crab–like' body plan is the plesiomorphic condition for the raninoidan clade as a whole (Chapter 3). The 'frog–like' architecture of most †Palaeocorystidae and of Raninoidea, with carapaces elongated, pleons partially exposed dorsally, and modified shovel-like podomeres of their pereiopods, reflect a highly derived condition related to a specialized back-burrowing lifestyle. The oldest orithopsids, cenomanocarcinid, and palaeocorystids — early stem-group raninoidans — indicate that the tropical Americas might have played an important role in the early radiation of the group during the Early Cretaceous, and challenge previous hypotheses about their high latitude origins.

Regarding the fossil record of Eubrachyura, the mid-Cretaceous family †Telamonocarcinidae is considered to be closer to Dorippidae and Ethusidae than to other brachyuran clades (Larghi, 2004; Luque, 2015b), and reinforces the hypothesis that Dorippoidea is among the most basal groups of eubrachyuran crabs (Chapter 2). †*Telamonocarcinus antiquus* from the early Albian is, together with †*Componocancer roberti* and putatively †*Tepexicarcinus tlayuaensis*, the oldest eubrachyuran-like crabs known to date, followed by the late Albian †*Cretamaja* Klompmaker, 2013, and †*Koskobilius* Klompmaker, 2013. The broad range of body plans seen among Albian brachyurans indicate that the Early Cretaceous was a time of rapid evolution not only for eubrachyurans, but for crabs in general, where most of the higher clades (e.g., †Callichimaeroida, †Etyoida, †Torynommoida, Raninoida, Cyclodorippoida, Eubrachyura) originated and/or diversified rapidly (Chapter 4). Given our current knowledge of the geographic and geological ranges of early eubrachyurans, I conclude that a) the oldest eubrachyurans are known from the Americas, b) eubrachyurans were already morphologically diverse in Albian times; and c) the most recent common ancestor of eubrachyurans most likely is pre–Albian in age, and probably rooted in the earliest Cretaceous or even the late Jurassic (Chapter 2).

The discovery of †*Callichimaera perplexa* in upper Cenomanian–lower Turonian rocks of Colombia and USA, respectively, reveals a novel podotreme body form restricted to the Cretaceous of the Americas so far. Its remarkable degree of preservation reveals the earliest adaptations for swimming/digging via paddle-like thoracic legs in crustaceans, which are unmatched among arthropods and only superficially similar to those seen in some eurypterids (sea scorpions), gyrinid beetles (whirligig beetles), some raninoidans (frog crabs and allies), matutids (moon crabs), and portunids (blue crabs). Flattened paddle-like legs have likely evolved several times in brachyurans via exaptation of flattened legs used for digging that were subsequently repurposed for active swimming (for example, as in portunid crabs). This striking 'chimaera' also seems to retain many larval features, such as an overall carapace form and large eyes lacking protective orbits, likely resulting from heterochronous development (paedomorphosis), which highlights the interplay between development and ecology in the evolution of novel forms and functions (Chapter 4). Morphological and stratigraphic data from all major true crab clades reveal an immense versatility of form during the Cretaceous, when nearly 80% of higher rank clades have their earliest known records, and suggest tropical oceans might have played a role as cradles for this diversification.

With respect to the distribution of visual systems across brachyuran taxa, reflecting superposition or ‘mirror’ eyes, characterized by square facets packed in a rectilinear lattice, are present in the oldest and less inclusive brachyuran superfamilies Dromioidea, Homolodromioidea, and Homoloidea. This supports the view that mirror eyes are the plesiomorphic condition for true crabs, and therefore present in the most recent common ancestor for crown Brachyura. More inclusive clades like Raninoidea and Cyclodorippoidea share with the ‘higher’ true crabs, or Eubrachyura, the expression in post-larval forms of eyes with hexagonal or roundish facets in hexagonal packing. Such eyes are either of the apposition, parabolic superposition, or refracting superposition type, and therefore reject the presence of mirror eyes present in lesser brachyuran branches (Chapter 6). Furthermore, the eyes of stem brachyurans like †Callichimaeroidea, †Necrocarcinoidea (e.g., †Cenomanocarcinidae: †*Cenomanocarcinus*), and †Etyoidea (e.g., †Feldmannidae: †*Caloxanthus*) are more similar to Raninoidea, Cyclodorippoidea and Eubrachyura than to Homolodromioidea, Dromioidea, and Homoloidea (Fig. 6.11). Therefore, the loss of mirror eyes in adults could have occurred once in a most recent common ancestor for †Callichimaeroidea, †Etyoidea, †Necrocarcinoidea, Raninoidea, Cyclodorippoidea, and Eubrachyura. However, this is a phylogenetic view of the distribution of visual systems in brachyurans, and the specific ecological conditions of several groups (e.g., colonization of fresh water, terrestrialization, diurnal activity, bathymetric range etc.), could have led to the independent loss of mirror eyes in many taxa, and multiple origins of parabolic and refracting superposition optics, making visual systems not phylogenetically informative at certain levels (e.g., above superfamily). In Eubrachyura and some podotreme brachyurans, the larval apposition eyes could be retained in adults due to paedomorphic fixation of megalopae apposition eyes, or exaptation of a pre-adapted larval apposition eye to function as parabolic or refracting eyes (Porter and Cronin, 2009). I conclude that the secondary retention of larval apposition eyes has existed in 'higher' podotremes and in eubrachyurans since at least the Early Cretaceous, and that the distribution of eye types among brachyuran crabs supports a paraphyletic podotreme grade increasing in complexity during the Cretaceous (Chapter 6).

The large unprotected and non-retractable eyes in †*Callichimaera* are unlike those of fossorial crabs like Raninoidea, and support a non-burrowing lifestyle (Chapters 4 and 6). The marginal region with squarish facets, seen only in one small specimen of †*Callichimaera*, may not indicate a regionalization of the eye but an artifact of the packing. Alternatively, if †*Callichimaera* is closer to earlier brachyurans like Homoloida, it might have secondarily suppressed the expression of mirror eyes in post-larvae and retain the larval apposition eyes. The presence of compound eyes with hexagonal facets packed in a hexagonal array in the extinct stem-raninoidan †Cenomanocarcinidae indicate that the loss of mirror eyes in stem and crown raninoidans must have occurred earlier than 90 Mya. Similarly, the presence of hexagonal facets and packing in the eyes of other fossil podotreme brachyuran lineages such as †Callichimaeroidea and †Etyoidea (~95 Mya) lead to the hypothesis that the loss of reflecting superposition eyes in adult brachyurans could have happened in a most recent common ancestor of †Callichimaeroida, †Etyoida, Raninoida, Cyclodorippoida, and Eubrachyura during the Early Cretaceous or earlier (Chapter 6). In agreement with previous findings (e.g., Porter and Cronin, 2009) the distribution of visual systems across crab taxa seems to be phylogenetically informative at lower levels like family or genera, but ecology appears to be the more important driver among higher taxa. Ongoing work aims to shed light on whether similar predictable "rules" account for the convergent origins and/or losses of apposition and mirror eye types among crabs through time.

7.2. Prospects and future directions

Disentangling the phylogenetic relationships across extinct and extant decapod groups is central to understanding the origins of novel forms and key innovations associated with carcinization and decarcinization across true and false crabs. Convergence, which potentially results in long-branch attractions, may be a result of similar underlying genetic, developmental and environmental factors, and similar predictable "rules" might account for the convergent origins and/or losses of body forms and visual systems among 'crabs' through time.

Using key fossil and extant taxa, together with histology, nano-CT scanning, and some phylogenetic techniques, I would like to reconstruct the evolution of the 'crab' body form across meiurans, and possibly explore transcriptomic data and potential loci affecting the expression of different eye types in post-larval stages. New fossils that I have collected, plus several recent findings, will provide updated age-calibration priors for divergence-time estimation, and serve as a backbone for node and tip dating.

Collectively, current and future findings might provide novel insights about the time, place, and phylogenetic pathways of early diversification in crabs, with the aim of contributing to the vast ongoing inter–institutional effort to resolve the Decapoda Tree of Life.

References

Abele, L. G., and Felgenhauer, B. E. 1982. Decapoda. In Parker, S. P. (Ed) *Synopsis and Classification of Living Organisms.* 2, 296-326 pp. New York. McGraw-Hill Book Co.

Acosta, C. E., Huertas, G. H., and Ruiz, P. M. 1979. Noticia preliminar sobre el Hallazgo de un presunto *Kronosaurus* (Reptilia: Dolichrorhynchopidae) en el Aptiano Superior de Villa de Leiva, Colombia. *Lozanía (Acta Zoologica Colombiana)*, 28: 1–7.

Agassiz, L. 1841. On the fossil fishes found by Mr Gardner in the Province of Ceari, in the north of Brazil. *Edinburgh New Philosophical Journal*, 30: 82-84.

Agnew, J. 2001. Taxonomy, taphonomy, and paleoecology of the Plio-Pleistocene shell beds at 101 Ranch Pit, Okeechobbe County, Florida (p. 219). University of Florida: Gainesville, Florida, USA.

Aguilera, O., Rodrigues de Aguilera, D., Vega, F. J., and Sánchez-Villagra, M. 2010. Mesozoic and Cenozoic decapod crustaceans from Venezuela and related trace-fossil assemblages. In Sánchez-Villagra, M., Aguilera, O. and Carlini, A. A. (Eds) *Urumaco and Venezuelan paleontology*, 103–128 pp. Indiana University Press.

Ahyong, S. T., and Baba, K. 2004. Chirostylidae from north-western Australia (Crustacea: Decapoda: Anomura). *Memoirs of Museum Victoria*, 61(1): 57–64.

Ahyong, S. T., and O'Meally, D. 2004. Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. *The Raffles Bulletin of Zoology*, 52(2): 673–693.

Ahyong, S. T., Lai, J. C. Y., Sharkey, D., Colgan, D. J., and Ng, P. K. L. 2007. Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): The status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution*, 45(2): 576–586.

Ahyong, S. T., Lowry, J. K., Alonso, M., Bamber, R. N., Boxshall, G. A., Castro, P., Gerken, S., Karaman, G. S., J.W., G., Jones, D. S., and al., e. 2011. Subphylum Crustacea Brünnich, 1772. In Zhang, Z. Q. (Ed) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*. Zootaxa 39: 165–191.

Ahyong, S. T., Lowry, J. K., Alonso, M., Bamber, R. N., Boxshall, G. A., Castro, P., Gerken, S., Karaman, G. S., Goy, J. W., Jones, D. S., Meland, K., Rogers, C., and Svavarsson, J. 2012. Subphylum Crustacea Brünnich, 1772. In Zhang, Z.-Q (Ed). Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, 3148: 165-191.

Alcock, A. 1896. Materials for a carcinological fauna of India. No. 2. The Brachyura Oxystoma. *Journal of the Asiatic Society of Bengal*, 65: 134-296, Plates VI-VIII.

Alcock, A. 1898. Materials for a carcinological fauna of India. No. 3. The Brachyura Cyclometopa. Part I. The family Xanthidae. *Journal of the Asiatic Society of Bengal*, 67(2): 67–233.

Alcock, A. 1900a. Materials for a carcinological fauna of India, No. 5. The Brachyura Primigenia or Dromiacea. *Journal of the Asiatic Society of Bengal*, 68((2)(3)): 123–169.

Alcock, A. 1900b. Materials for a carcinological fauna of India, No. 6. The Brachyura Catometopa, or Grapsoidea. *Journal of the Asiatic Society of Bengal*, 69(2–3): 279–456.

Anker, A., and Paulay, G. 2013. A remarkable new crab-like hermit crab (Decapoda: Paguridae) from French Polynesia, with comments on carcinization in the Anomura. *Zootaxa*, 3722(2): 8.

Anthula, D. J. 1899. Über die Kreidefossilien des Kaukasus mit einem allgemeinen Ueberblick über die Entwicklung der Sedimentärbildungen des Kaukasus. In Frech, F. and von Arthaber, G. (Eds) *Beiträge zur Paläontologie Österreich-Ungarns und des Orients.* 12, 55–159 pp. Wilhelm Braumüller.

Armstrong, A., Nyborg, T., Bishop, G. A., Ossó-Morales, À., and Vega, F. J. 2009. Decapod crustaceans from the Paleocene of Central Texas, USA. *Revsta Mexicana de Ciencias Geológicas*, 26(3): 745–763.

Arruda, D. C. B., and Abrunhosa, F. A. 2011. Redescription of megalopa and juvenile development of *Pachygrapsus gracilis* (Decapoda: Grapsidae) from the Amazon region, reared in the laboratory. *Zoologia (Curitiba)*, 28: 465–478.

Artal, P., Guinot, D., Van Bakel, B., and Castillo, J. 2008. Ibericancridae, a new dakoticancroid family (Decapoda, Brachyura, Podotremata) from the upper Campanian (Upper Cretaceous) of Spain. *Zootaxa*, 1907: 1–27.

Artal, P., Van Bakel, B. W. M., Fraaije, R. H. B., Jagt, J. W. M., and Klompmaker, A. A. 2012. New Albian-Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain. *Revista Mexicana de Ciencias Geológicas*, 29(2): 398-410.

Averof, M., and Patel, N. 1997. Crustacean appendage evolution associated with changes in Hox gene expression. *Nature*, 388: 682–686.

Baalbergen, E., and Donovan, S. K. 2013. Terrestrial arthropods from the Late Pleistocene of Jamaica: systematics, palaeoecology and taphonomy. *Geological Journal*, 48: 628–645.

Bell, T. 1836. Some account of the Crustacea of the coasts of South America, with descriptions of new genera and species, founded principally on the collections obtained by Mr. Cuming and Mr. Miller. (Tribus 1, Oxyrhynchi). *Proceedings of the Zoological Society of London*, 3 [1835]: 169–173.

Bell, T. 1855. Horae carcinologicae, or notices of crustacea. I. A monograph of the Leucosiidae, with observations on the relations, structure, habits and distribution of the family; a revision of the generic characters; and descriptions of new genera and species. *Transactions of the Linnean Society of London*, 21(277–314).

Bell, T. 1858. A monograph of the fossil malacostracous Crustacea of Great Britain. Part I. Crustacea of the London Clay. *Monograph of the Palaeontographical Society*, 10: i-viii, 1–44, 11 pls.

Bell, T. 1863. A monograph of the Fossil Malacostracous Crustacea of Great Britain. Part II. Crustacea of the Gault and Greensand. *Monograph of the Palaeontographical Society*, 14: vii + 40 pp., pls. 41–11.

Bellwood, O. 2002. The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). *Journal of Natural History*, 36(10): 1223–1238.

Bermúdez, H. D., Gómez-Cruz, A. d. J., Hyžný, M., Moreno-Bedmar, J. A., Barragán, R., Moreno, M., and Vega, F. J. 2013. Decapod crustaceans from the Cretaceous (Aptian-Albian) San Gil Group in the Villa de Leyva section, central Colombia. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 267(3): 255–272.

Beschin, C., Busulini, A., De Angeli, A., and Tessier, G. 1998. Raninidae del Terziario berico-lessineo (Italia settentrionale). *Lavori, Societa Veneziana di Scienza Naturali*, 13: 155–215.

Beurlen, K. 1930. Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschrifte in der Geologie und Paläontologie*, 8: 317–586.

Beurlen, K. 1932. Brachyurenreste aus dem Lias von Bornholm mit Beiträgen zur Phylogenie und Systematik der brachyuren Dekapoden. *Paläontologische Zeitschrift*, 14: 52–66.

Beurlen, K. 1958a. Contribuiçao à paleontologia do Estado do Para. Crustáceos decápodes da Formaçao Pirabas. I—(Arthropoda-Crustacea). *Boletim do Museu Paraense Emilio Goeldi*, 5: 1–48.

Beurlen, K. 1958b. Dois crustaceos do Cretáceo superior do nordeste do Brasil (Decapoda, Brachyura). *Boletim do Museu Nacional, Rio de Janeiro, (nova série)*, 26: 1–23.

Beurlen, K. 1965. Crustáceos Decápodos na Formaçao Riachuelo (Cretáceo–Sergipe). *Anais da Academia Brasiliera de Ciencias*, 37(2): 267–272.

Biffar, T. A., and Provenzano Jr, A. J. 1972. A reexamination of *Dardanus venosus* (H. Milne Edwards) and *D. imperator* (Miers), with a description of a new species of *Dardanus* from the western Atlantic (Crustacea, Decapoda, Diogenidae). *Bulletin of Marine Science*, 22(4): 777–805.

Bishop, G. A. 1978. Two new crabs, *Sodakus tatankayotankaensis* n. gen., n. sp. and *Raninella oaheensis* n. sp.(Crustacea, Decapoda), from the Upper Cretaceous Pierre Shale of South Dakota. *Journal of Paleontology*, 52(3): 608–617.

Bishop, G. A. 1983a. Two new species of crabs, *Notopocorystes* (*Eucorystes*) *eichhorni* and *Zygastrocarcinus griesi* (Decapoda: Brachyura) from the Bearpaw Shale (Campanian) of north-central Montana. *Journal of Paleontology*, 57: 900–910.

Bishop, G. A. 1983b. Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of central Texas. *Transactions of the San Diego Society of Natural History*, 20(2): 27–55.

Bishop, G. A. 1985. A new crab, *Prehepatus harrisi* (Crustacea, Decapoda) from the Coon Creek and Prairie Bluff formations, Union County, Mississippi. *Journal of Paleontology*, 59(5): 1028–1032.

Bishop, G. A. 1988. Two crabs, *Xandaros sternbergi* (Rathbun 1926) n. gen., and *Icriocarcinus xestos* n. gen., n. sp., from the late Cretaceous of San Diego County, California, USA, and Baja California Norte, Mexico. *Transactions of the San Diego Society of Natural History*, 21(5): 245–257.

Bishop, G. A., and Portell, R. W. 1989. Pliocene crab-sea star association from southwest Florida. *Journal of Crustacean Biology*, 9(3): 453–458.

Blow, W. C., and Manning, R. B. 1996. Preliminary descriptions of 25 new decapod crustaceans from the middle Eocene of the Carolinas, U.S.A. *Tulane Studies in Geology and Paleontology*, 29(1): 1–26.

Borradaile, L. A. 1903. Marine Crustaceans, 4. Some remarks on the classification of the crabs. 5. The crabs of catometope families. 6. The sand crabs (Oxystomata). *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, 1: 424-443.

Borradaile, L. A. 1916. Crustacea. Part II. Porcellanopagurus: An instance of carcinization. *British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report. Zoology*, 3(3): 111-126.

Bourne, G. C. 1922. On the Raninidae: a study in carcinology. *Journal of the Linnéan Society of London, Zoology*, 35: 25-79.

Bouvier, E. L. 1894. Sur l'appareil branchial d'un crabe du groupe des Dromiens, la *Dynomene filholi*. *Comptes rendus de la Société philomathique de Paris*, 7: 6.

Bouvier, E. L. 1899. *Calappa Zurcheri*, Crabe nouveau des terrains miocènes de Panama. *Bulletin du Muséum d'Histoire Naturelle, Paris*, 5: 189–192.

Bowen, B. W., Rocha, L. A., Toonen, R. J., and Karl, S. A. 2013. The origins of tropical marine biodiversity. *Trends in Ecology & Evolution*, 28(6): 359–366.

Boyko, C. B., and McLaughlin, P. A. 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part IV – Hippoidea. *The Raffles Bulletin of Zoology*, 23: 139–151.

Bracken-Grissom, H., Cannon, M., Cabezas, P., Feldmann, R., Schweitzer, C., Ahyong, S., Felder, D., Lemaitre, R., and Crandall, K. 2013. A comprehensive and integrative reconstruction of evolutionary history for Anomura (Crustacea: Decapoda). *BMC Evolutionary Biology*, 13(1): 128.

Brazeau, M. D. 2011. Problematic character coding methods in morphology and their effects. *Biological Journal of the Linnean Society*, 104(3): 489–498.

Breton, G. 2009. Description of *Priscinachus elongatus* n. gen., n. sp., and Priscinachidae n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian). *Geodiversitas*, 31(3): 509-523.

Brito, I. M. 1971. Contribuição ao conhecimento dos Crustáceos Decápodes da Formação Pirabas. I – Brachyura- Brachyrhyncha. *Anais da Academia Brasileira de Ciências*, 43: 489–498.

Brito, I. M. 1972. Contribuição ao Conhecimento dos Crustáceos Decápodos da Formação Pirabas. II — O Gênero *Uca* (Brachyura-Ocypodidae). *Anais da Academia Brasileira de Ciências*, 44(1): 95–98.

Brösing, A., Richter, S., and Scholtz, G. 2007. Phylogenetic analysis of the Brachyura (Crustacea, Decapoda) based on characters of the foregut with establishment of a new taxon. *Journal of Zoological Systematics and Evolutionary Research*, 45(1): 20–32.

Brullé, G. A. 1836–1850a. Crustacés. In Barker-Webb, P. and Berthelot, S. (Eds) *Histoire Naturelle des Îles Canaries.* Vol. 2 (Part 2), 15–18 pp. Paris: Béthune.

Brullé, M. 1836–1850b. Crustacés. In Barker-Webb, P. and Berthelot, S. (Eds) *Histoire Naturelle des Îles Canaries. Vol. 2 (Part 2)*, 13–18, 11 plate pp. Paris: Béthune.

Cáceres, C., Cediel, F., and Etayo, F. 2005. Maps of sedimentary facies distribution and tectonic setting of Colombia through the Proterozoic and Phanerozoic. Bogotá.

Cáceres, C., Rincón, A. D., Solórzano, A., Nuñez, M., Ruiz-Ramoni, D., and Sánchez, L. 2016. The first record of the extinct crab *Necronectes* (Decapoda: Portunidae) in Venezuela. *Revista Brasileira de Paleontologia*, 19(1): 145–148.

Carriol, R.-P., Muizon, C. d., and Secretán, S. 1987. Les crustacés (Cirripedia et Decapoda) du Néogène de la côte péruvienne. *Annales de Paléontologie, (Vert.-Invert.)*, 73(3): 137–164.

Casadío, S., De Angeli, A., Feldmann, R. M., Garassino, A., Hetler, J. L., Parras, A., and Schweitzer, C. E. 2004. New decapod crustaceans (Thalassinidea, Galatheoidea, Brachyura) from the middle Oligocene of Patagonia, Argentina. *Annals of Carnegie Museum*, 73: 25–47.

Castro, P. 2005. Crabs of the subfamily Ethusinae Guinot, 1977 (Crustacea, Decapoda, Brachyura, Dorippidae) of the Indo–West Pacific region. *Zoosystema*, 27: 499–593.

Chablais, J., Feldmann, R. M., and Schweitzer, C. E. 2011. A new Triassic decapod, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura. *Paläontologische Zeitschrift*, 85(1): 93–102.

Chace, F. A. 1939. Reports on the scientific results of the first Atlantic Expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary description of one new genus and seventeen new species of decapod and stomatopod Crustacea. *Memorias de la Sociedad Cubana de Historia Natural*, 13(1): 31–54.

Collins, J. S. H., and Morris, S. F. 1975. A new crab, *Costacopluma concava* from the Upper Cretaceous of Nigeria. *Palaeontology*, 18(4): 823–829.

Collins, J. S. H., and Morris, S. F. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad. *Palaeontology*, 19: 107–131.

Collins, J. S. H., and Rasmussen, H. W. 1992. Upper Cretaceous - Lower Tertiary decapod crustaceans from West Greenland. *Bulletin Grønlands Geologiske Undersøgelse*, 162: 1–46.

Collins, J. S. H., Kanie, Y., and Karasawa, H. 1993. Late Cretaceous Crabs from Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, (new series)*, 172: 292–310.

Collins, J. S. H., and Smith, R. 1993. Ypresian (Lower Eocene) crabs (Decapoda, Crustacea) from Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 63: 261–270, pl. 261.

Collins, J. S. H., Higgs, R., and Cortitula, B. 1994. A new crab, *Costacopluma bifida* (Crustacea, Decapoda) from the Palaeocene of Venezuela. *Bulletin of the Mizunami Fossil Museum*, 21: 29–34.

Collins, J. S. H., and Donovan, S. K. 1995. A new species of *Necronectes* (Decapoda) from the upper Oligocene of Antigua. *Caribbean Journal of Science*, 31(1–2): 122–127.

Collins, J. S. H., Donovan, S. K. v., and Dixon, H. L. 1997. Crabs and barnacles (Crustacea: Decapoda and Cirripedia) from the late Pleistocene Port Morant Formation of southeast Jamaica. *Bulletin of the Mizunami Fossil Museum*, 23: 51–63.

Collins, J. S. H., and Donovan, S. K. 1998. Some new crab records (Crustacea: Decapoda) from the late Pleistocene Port Morant Formation of southeast Jamaica. *Bulletin of the Mizunami Fossil Museum*, 24((for 1997)): 73–77.

Collins, J. S. H., and Portell, R. W. 1998. Decapod, stomatopod and cirripede Crustacea from the Pliocene Bowden shell bed, St. Thomas parish, Jamaica. *Contributions to Tertiary and Quaternary Geology*, 35(1–4): 113–127.

Collins, J. S. H., Donovan, S. K., Lindsay, W., and Stimpson, G. A. 2001. A new species of portunid crab from the Early Pleistocene Old Pera beds of Jamaica. *Proceedings of theGeologists' Association*, 112: 7–12.

Collins, J. S. H., and Donovan, S. K. 2002. A new species of calappid crab from the upper Oligocene of Antigua. *Caribbean Journal of Science*, 38(1–2): 145–146.

Collins, J. S. H., and Jakobsen, S. L. 2003. New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum*, 30: 63–96.

Collins, J. S. H., Lee, C., and Noad, J. 2003. Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Palaeontology*, 1(3): 187–226.

Collins, J. S. H., and Donovan, S. K. 2004. Decapod crustaceans from the Seroe Domi Formation (Mio-Pliocene) of Aruba, Netherlands Antilles. *Caribbean Journal of Science*, 40(3): 383–387.

Collins, J. S. H., and Donovan, S. K. 2005. Eocene crabs (Crustacea, Brachyura) from Bonaire, Netherlands Antilles. *Scripta Geologica*, 129: 1–12.

Collins, J. S. H., and Donovan, S. K. 2006. New decapod crustaceans from the Palaeogene of Jamaica. *Bulletin of the Mizunami Fossil Museum*, 33: 59–65.

Collins, J. S. H., Donovan, S. K., and Stemann, T. 2009a. Fossil Crustacea of the late Pleistocene Port Morant Formation, west Port Morant Harbour, southeastern Jamaica. *Scripta Geologica*, 138: 23–53.

Collins, J. S. H., Mitchell, S. F., and Donovan, S. K. 2009b. A new species of land crab, *Sesarma* Say , 1817(Decapoda, Brachyura), from the Pleistocene of Jamaica. *Scripta Geologica*, 138.

Collins, J. S. H., Portell, R. W., and Donovan, S. K. 2009c. Decapod crustaceans from the Neogene of the Caribbean: Diversity, distribution and prospectus. *Scripta Geologica*, 138: 55–111.

Collins, J. S. H., Donovan, S. K., Stemann, T. A., and Blissett, D. J. 2010. Crustaceans of the upper Miocene August Town Formation of southeastern Jamaica. *Scripta Geologica Special Issue, 7*: 177–183.

Collins, J. S. H., and Donovan, S. K. 2012. Pleistocene decapod crustaceans of eastern Jamaica. *Caribbean Journal of Science*, 46: 133–142.

Colosi, G. 1923. Una specie fossile de Gerionide (Decapodi brachiuri). *Bolettino della Societá dei Naturalisti in Napoli, Series 2*, 15(35): 248–255.

Crane, J. 1975. Fiddler Crabs of the World (Ocypodidae: genus *Uca*): Princeton University Press.

Cronin, T. W., and Porter, M. L. 2008. Exceptional variation on a common theme: The evolution of crustacean compound eyes. *Evolution: Education and Outreach*, 1(4): 463–475.

Cunningham, C., Blackstone, N., and Buss, L. 1992. Evolution of king crabs from hermit crab ancestors. *Nature*, 355: 539–542.

Dana, J. D. 1851a. Conspectus Crustaceorum quæ in Orbis Terrarum circumnavigatione, Carolo Wilkes e classe Reipublicæ Fœderatæ Duce, lexit et descripsit. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5: 247–254, 267–272.

Dana, J. D. 1851b. Conspectus Crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes, e Classe Reipublicae Foederatae Duce, lexit et descripsit. Pars VI. *American Journal of Science and Arts, Series 2*, 11(32): 268–274.

Dana, J. D. 1851c. On the classification of the Cancroidea. *American Journal of Science and Arts, Series 2*, 12: 121–131.

Dana, J. D. 1851d. On the classification of the maioid Crustacea or Oxyrhyncha. *American Journal of Science and Arts, Series 2*, 5(11): 425–434.

Dana, J. D. 1852. Parts I and II, Crustacea*United States Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N.* 13, 1–1620 pp. Philadelphia. C. Sherman.

Dana, J. D. 1853. On the classification and geographical distribution of Crustacea*Report on Crustacea of the United States Exploring Expedition, under Captain Charles Wilkes, U.S.N., during the years 1838–42. Philadelphia*, 395–1592 pp. C. Sherman.

Davie, P. J. F., Guinot, D., and Ng, P. K. L. 2015a. Anatomy and functional morphology of Brachyura*Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C (2 vols)*, 11-163 pp. Brill.

Davie, P. J. F., Guinot, D., and Ng, P. K. L. 2015b. Systematics and classification of Brachyura*Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C (2 vols)*, 1049-1130 pp. Brill.

Davie, P. J. F., Guinot, D., and Ng, P. K. L. 2015c. Phylogeny of Brachyura*Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C (2 vols)*, 921-979 pp. Brill.

Dawson, E. W., and Yaldwing, J. C. 2000. Description and ecological distribution of a new frog crab (Crustacea, Brachyura, Raninidae) from Northern New Zealand waters, with keys to Recent Raninid genera and *Notosceles* species. *Tuhinga*, 11: 47-71.

De Grave, S., Pentcheff, N. D., Ahyong, S. T., Chan, T. Y., Crandall, K. A., Dworschak, P. C., Felder, D. L., Feldmann, R. M., Fransen, C. H. J. M., Goulding, L. Y. D., Lemaitre, R., Low, M. E. Y., Martin, J. W., Ng, P. K. L., Schweitzer, C. E., Tan, S. H., Tshudy, D., and Wetzer, R. 2009. A classification of Recent and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology Supplement*, 21: 1–109.

De Haan, W. 1830–1850. Crustacea. In Siebold, P. F. v. (Ed) *Fauna Japonica sive Descriptio Animalium, Quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Noitis, Observationibus et Adumbrationibus Illustravit*, i-xvii, i-xxxi, ix-xvi, 1–243, pls. A–J, L–Q, 241–255, table 242 pp. Leiden. Lugduni-Batavorum.

De Haan, W. 1833–1850. Crustacea. In Siebold, P. F. v. (Ed) *Fauna Japonica sive Descriptio Animalium, Quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*, i-xvii, i-xxxi, ix-xvi, 1–243, pls. A–J, L–Q, 241–255, table 242 pp. Leiden. Lugduni-Batavorum.

DeBrosse, G., Sulkin, S., and Jamieson, G. 1990. Intraspecific morphological variability in megalopae of three sympatric species of the genus *Cancer* (Brachyura: Cancridae). *Journal of Crustacean Biology*, 10(2): 315–329.

Desmarest, A. G. 1823. Malacostracés, Malacostraca. (Crust.). In Cuvier, F. (Ed) *Dictionnaire des Sciences Naturelles, dans lequel on trait Méthodiquement des Différens étres de la Nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement a l'utilité qu'en peuvent retirer la Médecine, l'Agriculture, le Commerce et les Arts. Suivi d'une biographie des plus Célèbres Naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères génériques et spécifiques, leur lieu natal, leurs propiétés et leurs usages.* 28, 138–425 pp. Strasbourg et Paris. F.G. Levrault et Le Normant.

Dietl, G. P., and Vega, F. J. 2008. Specialized shell-breaking crab claws in Cretaceous seas. *Biology Letters*, 4(3): 290.

Domínguez Alonso, P. 2008. Nuevo cangrejo violinista (género *Uca*, Ocypodidae) en el Plio-Pleistoceno del litoral pacífico de Honduras. *Ameghiniana*, 45(4): 663–676.

Donovan, S. K., and Dixon, H. L. 1998. A fossil land crab from the late Quaternary of Jamaica (Decapoda, Brachyura, Gecarcinidae). *Crustaceana*, 71(7): 824–826.

Donovan, S. K., Pickerill, R. O. N., Portell, R., Jackson, T., and Harper, D. 2003. The Miocene palaeobathymetry and palaeoenvironments of Carriacou, the Grenadines, Lesser Antilles. *Lethaia*, 36(3): 255–272.

Donovan, S. K. 2016. Terrestrial arthropods from the Late Pleistocene of Jamaica – systematics, palaeoecology and taphonomy: supplement. *Geological Journal*.

Etayo-Serna, F. 1968a. Sinopsis Estratigráfica de la región de Villa de Leiva y zonas próximas. *Boletín de Geología Universidad Industrial de Santander*, 21: 19–32.

Etayo-Serna, F. 1968b. El Sistema Cretáceo en la región de Villa de Leiva y zonas próximas. *Geología Colombiana*, 5: 5–74.

Etayo-Serna, F. 1979. Zonation of the Cretaceous of central Colombia by ammonites. Bogotá, Colombia: Ministerio de Minas y Energia, Instituto Nacional de Investigaciones Geológico-Mineras.

Eudes-Deslongchamps, J. A. 1835. Mémoire pour servir à l'histoire naturelle des Crustacés fossils. *Mémoire de la Societé Linnéenne de Normandie*, 5: 37-46, pl. 31.

Fabiani, R. 1910. I crostacei terziarî del Vicentino. *Bolletin Museo Civico Vicenza*, 1(1): 29–45.

Fabricius, J. C. 1775. Systema Entomologiae, sistens Insectorum Classes, Ordines, Genera, Species, adjectis Sysnonymis, Locis, Descriptionibus, Observationibus. Flensburgi et Lipsiae: Officina Libraria Kortii.

Fabricius, J. C. 1777. Genera insectorum eorumque characteres naturales secundum numerum, figuram, situm et proportionem omnium partium oris adiecta mantissa specierum nuper detectarum. Litteris M.F. Bartschii: Chilonii.

Fabricius, J. C. 1787. Mantissa insectorum sistens eorum species nuper detec tas adjectis characteribus genericis, differentiis specifi cis, emenda tionibus, observationibus. Hafniae.

Feldmann, R. M., and Chirino-Galvez, L. 1991. First fossils of the decapod crustacean *Lyreidus* found in South America. *National Geographic Research and Exploration*, 7(4): 496–497.

Feldmann, R. M. 1992. The Genus *Lyreidus* de Haan, 1839 (Crustacea, Decapoda, Raninidae): Systematics and biogeography. *Journal of Paleontology*, 66(6): 943–957.

Feldmann, R. M., Chirino-Galvez, L., Mason, G. L., Anderson, J. L., Duncan, P. W., Ward, R. A., and Salem, D. R. 1993. Fossil Penaeidae (Crustacea: Decapoda) from the Loyola Formation, Ecuador. *Annals of Carnegie Museum*, 62: 229–243.

Feldmann, R. M., Tshudy, D. M., and Thomson, M. R. A. 1993. Late Cretaceous and Paleocene decapod crustaceans from James Ross Basin, Antarctic Peninsula. *Memoir (The Paleontological Society)*, 28(i-iv): 1–41.

Feldmann, R. M., and Martins Neto, R. G. 1995. *Costacopluma nordestina* n. sp. (Decapoda: Retroplumidae) from the Maria Farinha Formation (Paleocene) of Brazil. *Journal of Paleontology*, 69(3): 610–611.

Feldmann, R. M., Vega, F. J., Tucker, A. B., Garcia-Barrera, P., and Avendaño, J. 1996. The oldest record of *Lophoranina* (Decapoda: Raninidae) from the late Cretaceous of Chiapas, southeastern Mexico. *Journal of Paleontology*, 70(2): 296–303.

Feldmann, R. M., Bice, K. L., Hopkins, C. S., Salva, E. W., and Pickford, K. 1998a. Decapod crustaceans from the Eocene Castle Hayne Formation, North Carolina: Paleoceanographic implications. *Memoir (The Paleontological Society)*, 48: 1–28.

Feldmann, R. M., Vega, F. J., Applegate, S. P., and Bishop, G. A. 1998b. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology*, 72(1): 79–90.

Feldmann, R. M., Villamil, T., and Kauffman, E. G. 1999. Decapod and stomatopod crustaceans from mass mortality Lagerstatten: Turonian (Cretaceous) of Colombia. *Journal of Paleontology*, 73(1): 91–101.

Feldmann, R. M., and Villamil, T. 2002. A new carcineretid crab (Upper Turonian, Cretaceous) of Colombia. *Journal of Paleontology*, 76(4): 718–724.

Feldmann, R. M., and Schweitzer, C. E. 2004. Decapod Crustaceans from the lower Miocene of North-Western Venezuela (Cerro La Cruz, Castillo Formation). *Special Papers in Palaeontology*, 71: 7–22.

Feldmann, R. M., Schweitzer, C. E., and Encinas, A. 2005. New decapods from the Navidad Formation (Miocene) of Chile. *Journal of Crustacean Biology*, 25: 427–449.

Feldmann, R. M., and Schweitzer, C. E. 2006. Paleobiogeography of southern hemisphere decapod Crustacea. *Journal of Paleontology*, 80(1): 83-103.

Feldmann, R. M., Li, R.-Y., and Schweitzer, C. E. 2007. A new family, genus, and species of crab (Crustacea, Decapoda, Brachyura) from the upper Cretaceous (Campanian) of Manitoba, Canada. *Canadian Journal of Earth Sciences*, 44(12): 1741-1752.

Feldmann, R. M., and Portell, R. W. 2007. First record of *Costacopluma* Collins and Morris, 1975 (Decapoda: Brachyura: Retroplumidae) from the Eocene of Alabama, U.S.A. *Journal of Crustacean Biology*, 27(1): 90–96.

Feldmann, R. M., and Schweitzer, C. E. 2007. Sexual dimorphism in extinct and extant Raninidae (Decapoda: Brachyura). *Annals of Carnegie Museum*, 76(1): 39-52.

Feldmann, R. M., Schweitzer, C. E., and Green, R. M. 2008a. Unusual Albian (Early Cretaceous) Brachyura (Homoloidea: Componocancroidea new superfamily) from Montana and Wyoming, USA. *Journal of Crustacean Biology*, 28(3): 502–509.

Feldmann, R. M., Schweitzer, C. E., and Wahl, W. 2008b. *Ekalakia* (Decapoda: Brachyura): The preservation of eyes links Cretaceous crabs to Jurassic ancestors. *Journal of Paleontology*, 82(5): 1030–1034.

Feldmann, R. M., and Schweitzer, C. E. 2010a. The Oldest Shrimp (Devonian: Famennian) and Remarkable Preservation of Soft Tissue. *Journal of Crustacean Biology*, 30(4): 629-635.

Feldmann, R. M., and Schweitzer, C. E. 2010b. Is *Eocarcinus* Withers, 1932, a Basal Brachyuran? *Journal of Crustacean Biology*, 30(2): 241-250.

Feldmann, R. M., Schweitzer, C. E., and Encinas, A. 2010. Neogene decapod Crustacea from Southern Chile. *Annals of Carnegie Museum*, 78(4): 337–366.

Fincham, A. A. 1980. Eyes and classification of malacostracan crustaceans. *Nature*, 287(5784): 729-731.

Fincham, A. A. 1984. Ontogeny and optics of the eyes of the common prawn *Palaemon* (*Palaemon*) *serratus* (Pennant, 1777). *Zoological Journal of the Linnaean Society*, 81.

Flores, A., and Negreiros-Fransozo, M. L. 1999. Allometry of the secondary sexual characters of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). *Crustaceana*, 72(9): 1051–1066.

Förster, R. 1968. *Paranecrocarcinus libanoticus* n. sp. (Decapoda) und die Entwicklung der Calappidae in der Kreide. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, 8: 167–195.

Förster, R., and Stinnesbeck, W. 1987. Zwei neue Krebse, *Callianasssa saetosa* n. sp. und *Homolopsis chilensis* n. sp. (Crustacea, Decapoda) aus der Oberkreide Zentral-Chiles. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, 27: 51–65.

Fraaije, R. H., Vega, F. J., Van Bakel, B. W. M., and Garibay-Romero, L. M. 2006. Late Cretaceous dwarf decapods from Guerrero, southern Mexico and their migration patterns. *Contributions to Zoology*, 75(3/4): 121–132.

Fraaije, R. H. B., van Bakel, B. W. M., Jagt, J. W. M., and Artal, P. 2008. New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. *Annie V. Dhondt Memorial Volume: Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 78: 193-208.

Fraaije, R. H., Van Bakel, B. W. M., Jagt, J. W. M., and Viegas, P. A. 2018. The rise of a novel, plankton-based marine ecosystem during the Mesozoic: a bottom-up model to explain new higher-tier invertebrate morphotypes. *Boletín de la Sociedad Geológica Mexicana*, 70(1).

Freminville, M. d. 1835. Notice sur les tourlourouxou crabes de terre des Antilles. *Annales des Sciences Naturelles (2nd series)*, 3: 213–224.

Garassino, A., De Angeli, A., and Pasini, G. 2008. New decapod assemblage from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, 149(1): 37–67.

Garassino, A., Pasini, G., Porras-Múzquiz, H., and Vega, F. J. 2013. *Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Crustacea, Decapoda, Brachyura, Cenomanocarcinidae) from the Late Cretaceous (Turonian) of Morocco. *Boletín de la Sociedad Geológica Mexicana*, 65(2): 299–305.

Garth, J. S. 1958. Brachyura of the Pacific coast of America: Oxyrhyncha. *Allan Hancock Pacific Expeditions*, 21(1): 1–499.

Gaten, E., and Herring, P. J. 1995. Morphology of the reflecting superposition eyes of larval oplophorid shrimps. *Journal of Morphology*, 225(1): 19-29.

Gaten, E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contributions to Zoology*, 67(4): 223–236.

Gaten, E., Herring, P. J., Shelton, P. M. J., and Johnson, M. L. 1998. Comparative morphology of the eyes of postlarval bresiliid shrimps from the region of hydrothermal vents. *Biological Bulletin*, 194(3): 267–280.

Gelman, A., and Rubin, D. B. 1992. Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science*, 7(4): 457-472.

Gill, T. 1894. A new Bassalian type of crabs. *American Naturalist*, 28: 1043–1045.

Gistel, J. 1848. Naturgeschichte des Thierreiches für höhere Schulen bearbeitet. Stuttgart. xvi.

Glaessner, M. F. 1928. Die Dekapodenfauna des österreichischen Jungtertiärs. *Jahrbuch der Geologischen Bundesanstalt Wien*, 78: 161–219.

Glaessner, M. F. 1960. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Royal Society of South Australia, Transactions*, 104: 171-192.

Glaessner, M. F. 1969. Decapoda. In (ed.), R. C. M. (Ed) *Treatise on Invertebrate Paleontology. Part R. Arthropoda.* 4(2), R399-R651 pp. Geological Society of America and University of Kansas Press, Lawrence.

Glaessner, M. F. 1980. New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia*, 104(6): 171–192.

Goeke, G. D. 1981. Symethinae, new subfamily, and *Symethis garthi*, new species, and the transfer of *Raninoides ecuadorensis* to *Notosceless* (Raninidae: Brachyura: Gymnopleura). *Proceedings of the Biological Society of Washington*, 93(4): 971–981.

Goeke, G. D. 1985. Decapod Crustacea: Raninidae. Res. Camp. MUSORSTOM I-II. Philippines (1976, 1980), 2. *Mémoires du Muséum National d'Histoire Naturelle, Paris (A, Zoologie)*, 133: 205–228.

Goloboff, P. A., Farris, J. S., and K., N. 2008a. TNT, a free program for phylogenetic analysis. *Cladistics*, 24: 774–786.

Goloboff, P. A., Farris, J. S., and Nixon, K. C. 2008b. TNT, a free program for phylogenetic analysis. *Cladistics*, 24(5): 774-786.

Gomez, A. J., Bermudez, H., and Vega, F. J. 2015. A new species of *Diaulax* Bell, 1863 (Brachyura: Dialucidae) in the Early Cretaceous of the Rosablanca Formation, Colombia. *Boletín de la Sociedad Geológica Mexicana*, 67(1): 103–112.

Gordon, I. 1966a. On the spermatheca in the Raninidae (Crustacea: Decapoda). In Barnes, H. (Ed) *Some Contemporary Studies in Marine Science*, 343-354 pp.

Gordon, W. A. 1966b. Two crab species from the middle Tertiary of Puerto Rico. Transactions of the Third Caribbean Geological Conference, Kingston, Jamaica: 184–186.

Gould, C. 1859. Description of a new fossil crustacean from the lower Greensand. *Quarterly Journal of the Geological Society*, 15: 237–238.

Grossouvre, A. D. 1894. Recherches sur la craie supérieure. Partie 2. Paléontologie. Les ammonites de la craie supérieure. *Mémoires por servir à l'explication de la Carte Géologique Détaillée de la France*: 264.

Guerao, G., Díaz, D., and Abello, P. 2006. Morphology of puerulus and early juvenile stages of the spiny lobster *Palinurus mauritanicus* (Decapoda: Palinuridae). *Journal of Crustacean Biology*, 26(4): 480–494.

Guerao, G., and Rotllant, G. 2009. Post-larval development and sexual dimorphism of the spider crab *Maja brachydactyla* (Brachyura: Majidae). *Scientia Marina*, 73(4): 797–808.

Guerao, G., Anger, K., Simoni, R., and Cannicci, S. 2012. The early life history of *Chiromantes ortmanni* (Crosnier, 1965)(Decapoda: Brachyura: Sesarmidae): Morphology of larval and juvenile stages. *Zootaxa*, 3347: 1–35.

Gueriau, P., Charbonnier, S., and Clément, G. 2014. First decapod crustaceans in a Late Devonian continental ecosystem. *Palaeontology*, 57(6): 1203–1213.

Guinot, D. 1967. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. II. Les anciens genres *Micropanope* Stimpson et *Medaeus* Dana. *Bulletin du Muséum national d'Histoire naturelle, Paris, 2e série*, 39(2): 345–374.

Guinot, D. 1969. Sur divers Xanthidae, notamment sur *Actaea* de Haan et *Paractaea* gen. nov. (Crustacea Decapoda Brachyura). *Cahiers du Pacifique*, 13: 223–267.

Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes rendus hebdomadaires des séances de l'Académie des sciences*, 285(Série D): 1049–1052.

Guinot, D. 1991. Établissement de la famille des Poupiniidae pour *Poupina hirsuta* gen. nov., sp. nov. de Polynésie (Crustacea Decapoda Brachyura Homoloidea). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 12(4): 577–605.

Guinot, D. 1993. Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata). *Comptes Rendus de l'Académie des Sciences (Paris), Sciences de la vie*, 3(316): 1324–1331.

Guinot, D., and Richer de Forges, B. 1995. Crustacea Decapoda Brachyura: révision de la famille des Homolidae de Haan, 1839. *Résultats des campagnes MUSORSTOM*, 13: 283–517.

Guinot, D., and Tavares, M. 2001. Une nouvelle famille des crabs du Crustacés et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema*, 23: 507–546.

Guinot, D., and Tavares, M. 2003. A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and descriptions of new genera and species (Crustacea, Decapoda, Brachyura). *Zoosystema*, 25(1): 43–129.

Guinot, D., and Quenette, G. 2005. The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications. *Zoosystema*, 27(2): 267–342.

Guinot, D., and Breton, G. 2006. *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura). *Geodiversitas*, 28(4): 591–633.

Guinot, D. 2008. A re-evaluation of the Dynomenidae Ortmann, 1892 (Crustacea, Decapoda, Brachyura, Podotremata), with the recognition of four subfamilies. *Zootaxa*, 1850: 1–26.

Guinot, D., Vega, F. J., and Van Bakel, B. W. M. 2008. Cenomanocarcinidae n. fam., a new Cretaceous podotreme family (Crustacea, Decapoda, Brachyura, Raninoidia), with comments on related families. *Geodiversitas*, 30(4): 681–719.

Guinot, D., Tavares, M., and Castro, P. 2013. Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa*, 3665(1): 1–414.

Guppy, R. J. L. 1909. Preliminary notice of a discovery of fossils in the Tamana District, Trinidad. *Bulletin of the Agricultural Department, Trinidad*, 1909: 5–7.

Guzmán, W., Bermúdez, H., Gómez-Cruz, A., and Vega, F. J. 2016. *Ophthalmoplax* (Decapoda: Brachyura: Portunoidea) from the late Campanian, Upper Cretaceous, of Colombia. *Boletín de la Sociedad Geológica Colombiana*, 68(2): 375–376.

Hampe, O. 1992. Ein groBwüchiger Pliosauridae (Reptilia: Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien. *Courier Forschungsintitut Senckenberg*, 145: 1–27.

Hampe, O. 2005. Considerations on a *Brachauchenius* skeleton (Pliosauroidea) from the lower Paja Formation (late Barremian) of Villa de Leyva area (Colombia). *Fossil Record*, 8(1): 37–51.

Harlioglu, M. M. 2003. Differences in the crista dentata structure of the ischium of third maxilliped in *Astacus leptodactylus* (Eschscholtz, 1823). *Folia Biologica (Kraków)*, 51: 111–116.

Harlioglu, M. M. 2008. A scanning electron microscopic study on the appendage morphology of *Astacus leptodactylus* (Eschscholtz, 1823) and *Pacifastus leniusculus* (Dana, 1852) (Crustacea: Decapoda: Astacoidea). *International Journal of Morphology*, 26(4): 1035–1051.

Harrison, L. B., and Larsson, H. C. 2015. Among-character rate variation distributions in phylogenetic analysis of discrete morphological characters. *Systematic Biology*, 64(2): 307-324.

Hartnoll, R. G. 1971a. *Sesarma cookei* n. sp., a grapsid crab from Jamaica (Decapoda: Brachyura). *Crustaceana*, 20: 257–262.

Hartnoll, R. G. 1971b. The occurrence, methods and significance of swimming in the Brachyura. *Animal Behaviour*, 19(1): 34-50.

Harvey, A., Boyko, C. B., McLaughlin, P. A., and Martin, J. W. 2014. Anomura. In Martin, J. W., Olesen, J. and Høeg, J. T. (Eds) *Atlas of Crustacean Larvae*, 283–294 pp. Baltimore. Johns Hopkings University Press.

Haug, C., and Haug, J. T. 2016. Developmental paleontology and paleo-evo-devo. *Encyclopedia of Evolutionary Biology*, 1: 420–429.

Haug, J. T., Martin, J. W., and Haug, C. 2015. A 150-million-year-old crab larva and its implications for the early rise of brachyuran crabs. *Nature Communications*, 6: 2–6.

Haworth, A. H. 1825. A new binary arrangement of the macrurous Crustacea. *The Philosophical Magazine and Journal*, 65: 183–184.

Henderson, J. R. 1888. Report on the Anomura collected by H. M. S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of HMS Challenger (Zoology)*, 27(i–xi): 1–221.

Hendrickx, M. E. 1995. Checklist of the brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Bulletin de l'institut royal des Sciences Naturelles de Belgique, Biologie*, 65: 125–150.

Herbst, J. F. W. 1782–1804. Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten: Strals und GA Lange.

Hernández-Monzón, O., Vega, F. J., and Coutiño, M. A. 2007. A review of *Lophoranina cristaspina* from the Middle Eocene of Chiapas, México and evolutionary implications. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 35(2): 56–58.

Hiller, A., Viviani, C. A., and Werding, B. 2010. Hypercarcinisation: An evolutionary novelty in the commensal porcellanid *Allopetrolisthes spinifrons* (Crustacea: Decapoda: Porcellanidae). *Nauplius*, 18(1): 95-102.

Hines, A. H. 1986. Larval patterns in the life histories of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Bulletin of Marine Science*, 39(2): 444–466.

Hoedemaeker, P. J. 2004. On the Barremian-lower Albian stratigraphy of Colombia. *Scripta Geologica*, 128: 3–15.

Holland, F. D., Jr., and Cvancara, A. M. 1958. Crabs from the Cannonball Formation (Paleocene) of North Dakota. *Journal of Paleontology*, 32(3): 495-505.

Hoyoux, C., Zbinden, M., Samadi, S., Gaill, F., and Compère, P. 2009. Wood-based diet and microflora of a galatheid crab associated with Pacific deep-sea wood falls. *Marine Biology*, 156: 2421–2439.

Huertas, G. 1967. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. *Caldasia*, X(46): 60–75.

Huertas, G. 1970. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. *Caldasia*, X(50): 596–602.

Huertas, G. 1976. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. *Caldasia*, XI(54): 18–23.

Hyatt, A. 1903. Pseudoceratites of the Cretaceous. In Stanton, T. W. (Ed) *US Geological Survey Monographs.* 44, 351 p.

Ivany, L. C., Portell, R. W., and Jones, D. S. 1990. Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida. *Palaios*, 5: 244–258.

Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. *Nature*, 364(6433): 142-144.

Jablonski, D. 2005. Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 304(6): 504–519.

Jablonski, D., Roy, K., and Valentine, J. W. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314(5796): 102-106.

Jacob, C. 1907. Études paléontologiques et stratigraphiques sur la partie moyenne des terrains crétacés dans les Alpes françaises et les régions voisines (p. 314). Grenoble.

Jagt, J. W. M., Fraaije, R. H. B., Van Bakel, B. W. M., and Artal, P. 2010. *Necrocarcinus ornatissimus* Forir, 1887, and *Prehepatus werneri* Fraaye & Collins, 1987 (upper Maastrichtian, The

Netherlands) revisited, with notes on other Cretaceous Dynomenid crabs (Decapoda, Brachyura)*Studies on Brachyura: a Homage to Danièle Guinot*, 173–196 pp.

Jagt, J. W. M., Fraaije, R. H. B., and Van Bakel, B. W. M. 2014. Decapod crustacean 'odds and ends' from the Maastrichtian type area (southeast Netherlands, northeast Belgium). In Fraaije, R. H. B., Hyžný, M., Jagt, J. W. M., Krobicki, M. and Van Bakel, B. W. M. (Eds) *Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013, A tribute to Pál Mihály Müller. Scripta Geologica.* 147, 95–115 pp.

Jagt, J. W. M., Van Bakel, B. W. M., Guinot, D., Fraaije, R. H., and Artal, P. 2015. Fossil Brachyura. In Castro, P., Davie, P. J. F., Guinot, D., Schram, F. R. and Vaupel Klein, J. C. v. (Eds) *Decapoda: Brachyura (Part 2). Treatise on Zoology — Anatomy, Taxonomy, Biology. The Crustacea, Vol. 9C-*. 9C-II, 847–920 pp. Leiden & Boston. Brill.

Jamieson, B. G. M., Guinot, D., and Richer de Forges, B. 1995. Phylogeny of the Brachyura (Crustacea, Decapoda): Evidence from spermatozoal ultrastructure. In Jamieson, B. G. M., Ausio, J. and Justine, J.-L. (Eds) *Advances in Spermatozoal Phylogeny and Taxonomy. Mémoires du Muséum National d'Histoire Naturelle*, 166, 265–283 pp. Paris.

Jones, W. T., Feldmann, R. M., Schweitzer, C. E., Schram, F. R., Behr, R.-A., and Hand, K. L. 2014. The first Paleozoic stenopodidean from the Huntley Mountain Formation (Devonian–Carboniferous), north-central Pennsylvania. *Journal of Paleontology*, 88(6): 1251—1256.

Jordan, D. S., and Branner, J. C. 1908. The Cretaceous fishes of Ceara, Brazil. *Smithsonian Miscellaneous Collection*, 52(1): 1–29.

Julivert, M. 1968. Lexique Stratigraphique International. France: Centre National de la Recherche Scientifique.

Karasawa, H. 1990. Decapod crustaceans from the Miocene Mizunami Group, central Japan, Part 2 Section Oxyrhyncha, Cancridea and Brachyrhyncha. *Bulletin of the Mizunami Fossil Museum*, 17: 1–34.

Karasawa, H., and Kato, H. 2003. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): Systematics, phylogeny, and fossil records. *Paleontological Research*, 7(2): 129–151.

Karasawa, H., Schweitzer, C. E., and Feldmann, R. M. 2008. Revision of the Portunoidea Rafinesque, 1815 (Decapoda: Brachyura) with emphasis on the fossil genera and families. *Journal of Crustacean Biology*, 28(1): 82–127.

Karasawa, H., Schweitzer, C. E., and Feldmann, R. M. 2011. Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. *Journal of Crustacean Biology*, 31(3): 523–565.

Karasawa, H., Schweitzer, C. E., Feldmann, R. M., and Luque, J. 2014. Phylogeny and classification of the Raninoida (Decapoda: Brachyura). *Journal of Crustacean Biology*, 34(2): 216–272.

Kiel, S., and Hansen, B. T. 2015. Cenozoic methane-seep faunas of the Caribbean region. *PLoS One*, 10(10): e0140788.

Kiessling, W., Simpson, C., and Foote, M. 2010. Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, 327(5962): 196-198.

Klaus, S., Magalhães, C., Salas-Gismondi, R., Gross, M., and Antoine, P.-O. 2017. Paleogene and Neogene brachyurans of the Amazon Basin: A revised first appearance date for primary freshwater crabs (Crustacea, Brachyura, Trichodactylidae). *Crustaceana*, (Special Issue: Volume in Honour of Michael Türkay).

Klompmaker, A. A. 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: Implications for Cretaceous decapod paleoecology. *Cretaceous Research*, 41: 150-185.

Klompmaker, A. A., Flores-Ventura, J., and Vega, F. J. 2013a. A new homolid crab, *Zygastrocarcinus carolinasensis* n. sp., from the Cretaceous (Campanian) of NE Mexico: implications for paleobiogeography. *Boletín de la Sociedad Geológica Mexicana*, 65(2): 265–271.

Klompmaker, A. A., Karasawa, H., Portell, R. W., Fraaije, R. H. B., and Ando, Y. 2013b. An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *Palaios*, 28: 599–613.

Klompmaker, A. A., Portell, R. W., Klier, A. T., Prueter, V., and Tucker, A. L. 2015a. Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracidae. *PeerJ*, 3:e1301.

Klompmaker, A. A., Schweitzer, C. E., Feldmann, R. M., and Kowalewski, M. 2015b. Environmental and scale-dependent evolutionary trends in the body size of crustaceans. *Proceedings of the Royal Society of London B: Biological Sciences*, 282(1811).

Klompmaker, A. A., Chistoserdov, A. Y., and Felder, D. L. 2016a. Possible shell disease in 100 million-year-old crabs. *Diseases of Aquatic Organisms*, 119: 91–99.

Klompmaker, A. A., Hyžný, M., Portell, R. W., and Kowalewski, M. 2016b. Growth, inter- and intraspecific variation, palaeobiogeography, taphonomy and systematics of the Cenozoic ghost shrimp *Glypturus*. *Journal of Systematic Palaeontology*, 14(2): 99–126.

Klompmaker, A. A., Portell, R. W., and Frick, M. G. 2017. Comparative experimental taphonomy of eight marine arthropods indicate distinct differences in preservation potential. *Palaeontology*.

Krobicki, M., and Zatoń, M. 2008. Middle and Late Jurassic roots of brachyuran crabs: Palaeoenvironmental distribution during their early evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 263(1–2): 30-43.

Krøyer, H. 1837. *Geryon tridens*, en ny Krabbe. *Naturhistorisk Tidsskrift, series 1*, 1: 10–21.

Lamarck, J. B. P. A. 1801. Système des animaux sans vertébrés, ou tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leurs distribution, d'après la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du cours de zoologie, donné dans le Muséum national d'Histoire naturelle l'an 8 de la République. Déterville, Paris.

Lamarck, J. B. P. A. 1818. Histoire Naturelle des Animaux Sans Vertèbres. Tome 5: 612.

Land, M. F. 1976. Superposition images are formed by reflection in the eyes of some oceanic decapod crustacea. *Nature*, 263: 764–765.

Land, M. F. 1980. Compound eyes: old and new optical mechanisms. *Nature*, 287(681–686).

Land, M. F. 2000. Eyes with mirror optics. *Journal of Optics A: Pure and Applied Optics*, 2(6): R44.

Lanphere, M. A., and Jones, D. L. 1978. Cretaceous time scale from North America, in the geologic time scale. *AAPG Studies Geology*, 6: 259–268.

Larghi, C. 2004. Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology*, 78(3): 528–541.

Latreille, P. A. 1802. Histoire Naturelle, générale et particulière des Crustacés et des Insectes : Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et Partie du Cours complet d'Histoire Naturelle rédigé par C. S. Sonnini, Membre de plusieurs Sociétés Savantes. Paris: F. Dufart.

Latreille, P. A. 1817. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Paris: Déterville.

Latreille, P. A. 1819. Nouveau dictionnaire d'histoire naturelle appliquée aux arts, à l'agriculture, à l'économie rural et domestique, à la médecine, etc. . . (nouvelle édition presqu'entièrement refondue et considérablement augmentée; avec des figures tirées des trois règnes de la nature). Paris.

Latreille, P. A. 1825. Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. Paris: J. B. Baillière.

Latreille, P. A. 1825–1828. Encyclopédie méthodique, Histoire naturelle: Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes. Imprimerie-Libraire, Paris: Chez Mme veuve Agasse.

Latreille, P. A. 1829. Crustacés, arachnides et partie des insectes. (2nd Edition). In Cuvier, G. (Ed) *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des* *animaux et d'introduction à l'anatomie comparée. Nouvelle édition, revue et augmentée.* 4, 1–584 pp. Paris. Chez Déterville, Libraire; et Chez Crochard, Libraire.

Leach, W. E. 1813–1815. Crustaceology. In Webster, D. (Ed) *The Edinburgh Encyclopædia.* 7, 383–384 [1813], 1385–1437, 1765–1766 [1814], Plate 1221 [1815]. pp. Edinburgh, Balfour.

Leach, W. E. 1815. The zoological miscellany; being descriptions of new, or interesting animals. Covent Garden and London: E. Nodder and Son.

Leach, W. E. 1816. A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the distribution of the genera comprising three of these classes into orders, and descriptions of several new genera and species. *Transactions of the Linnean Society of London*, 11(2): 306–400.

Leach, W. E. 1816 [imprint 1815]. The zoological miscellany; being descriptions of new, or interesting animals. Covent Garden and London: E. Nodder and Son.

Leach, W. E. 1817. Monograph on the genera and species of the malacostracous family Leucosidea. In Leach, W. E. (Ed) *The Zoological Miscellany; being descriptions of new, or interesting animals.* 3, 17–26 pp. Covent Garden and London. E. Nodder and Son.

Lewis, J. E., and Ross, A. 1965. Notes on the Eocene Brachyura of Florida. *Quaterly Journal of the Florida Acedemy of Sciences*, 23(3): 233–244.

Lewis, P. O. 2001. A Likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6): 913-925.

Linnaeus, C. v. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Holmiae: Laurentii Salvii.

Locatelli, E. R. 2013. Preservation potential of gecarcinid land crabs (Decapoda, Brachyura, Gecarcinidae) from San Salvador. *Palaios*, 28(12): 867–874.

Lockington, W. N. 1877. Remarks on the Crustacea of the west coast of North America, with a catalogue of the species in the Museum of the California Academy of Sciences. *Proceedings of the California Academy of Sciences*, 7 [for 1876]: 94–108.

Lőrenthey, E. 1907. Palaeontologiai tanulmányok a harmadkorú rákok köréből. V. Adatok Egyptom eocenkori rákfaunájához. *Mathematikai és Természettudományi Közlemények*, 29(2): 195–242.

Lőrenthey, E., and Beurlen, K. 1929. Die fossilen Decapoden der Länder der Ungarischen Krone. *Geologica Hungarica (Palaeontologica)*, 3: 1–421, 412 tables, 416 pls.

Luque, J., Feldmann, R. M., Schweitzer, C. E., Jaramillo, C., and Cameron, C. B. 2012. The oldest frog crabs (Decapoda: Brachyura: Raninoida) from the Aptian of northern South America. *Journal of Crustacean Biology*, 32(3): 405–420.

Luque, J., Feldmann, R. M., Schweitzer, C. E., Karasawa, H., and Jaramillo, C. 2013. On the origin and evolution of true crabs: Insights from northern South America Geological Society of America Annual Meeting: 125th Anniversary of GSA.

Luque, J. 2014a. A new genus and species of raninoidian crab (Decapoda, Brachyura), from the Lower Cretaceous of Colombia, South America. *Scripta Geologica*, 147: 27–34.

Luque, J. 2014b. A new genus and species of raninoidian crab (Decapoda, Brachyura), from the Lower Cretaceous of Colombia, South America. In Fraaije, R. H. B., Hyžný, M., Jagt, J. W. M., Krobicki, M. and Van Bakel, B. W. M. (Eds) *Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. Scripta Geologica.* . 147, 27–34 pp.

Luque, J. 2015a. A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: Frog first or crab first? *Journal of Systematic Palaeontology*, 13(2): 153–166.

Luque, J. 2015b. The oldest higher true crabs (Crustacea: Decapoda: Brachyura): insights from the Early Cretaceous of the Americas. *Palaeontology*, 58(2): 251–263.

Luque, J., Hendy, A. J. W., Rosenberg, M. S., Portell, R. W., and Palmer, A. R. 2015. Cenozoic inter-tidal, supra-tidal, and freshwater crabs from Tropical America. Geological Society of America (GSA) Annual Meeting, Abstracts with Programs, 47: 423.

Luque, J. 2017. Fossil hermit and land crabs (Anomura and Brachyura) from the Quaternary of Antigua and Bermuda. *Journal of Crustacean Biology*, 37(2): 151–156.

Luque, J., Christy, J. H., Hendy, A. J. W., Rosenberg, M. S., Portell, R. W., Kerr, K. A., and Palmer, A. R. 2017a. Quaternary intertidal and supratidal crabs (Decapoda, Brachyura) from tropical America and the systematic affinities of fossil fiddler crabs. *Journal of Systematic Palaeontology*: 1-19.

Luque, J., Schweitzer, C. E., Santana, W., Portell, R. W., Vega, F. J., and Klompmaker, A. A. 2017b. Checklist of fossil decapod crustaceans from tropical America, Part I: Anomura and Brachyura. *Nauplius*, 25: e2017025.

Luque, J., Christy, J. H., Hendy, A. J. W., Rosenberg, M. S., Kerr, K. A., Portell, R. W., and Palmer, A. R. in press. Quaternary intertidal and supratidal fossil crabs (Decapoda, Brachyura) from tropical America and the systematic affinities of fossil fiddler crabs. *Journal of Systematic Palaeontology*.

M'Coy, F. 1849. On the classification of some British fossil Crustacea with notices of new forms in the university collection at Cambridge. *Annals and Magazine of Natural History*, 4(2): 161–179, 330–335.

MacLeay, W. S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In Smith, A. (Ed) *Illustrations of the Annulosa of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa. . ."*, 53–71 pp. London. Smith, Elder and Company.

Maddison, W. P., and Maddison, D. R. 2011. Mesquite: a modular system for evolutionary analysis. *Ver. 2.75*. http://mesquiteproject.org.

Magalhães, C. 2003. Famílias Pseudothelphusidae e Trichodactylidae. In Melo, G. A. S. (Ed) *Manual de Identificação dos Crustáceos Decápodos de Água Doce do Brasil. 1ªed*, 143–287 pp. São Paulo. Edições Loyola.

Maisey, J. G. 1991. Santana Fossils. An Illustrated Atlas: Neptune, NJ: T.F.H. Publications.

Maisey, J. G. 1994. Predator-prey relationships and trophic level reconstruction in a fossil fish community. *Environmental Biology of Fishes*, 40(1): 1–22.

Maisey, J. G., and Carvalho, M. d. G. P. d. 1995. First records of fossil sergestid decapods and fossil brachyuran crab larvae (Arthropoda, Crustacea), with remarks on some supposed palaemonid fossils, from the Santana Formation (Aptian-Albian, NE Brazil). *American Museum Novitates*, 3132: 1–17.

Mann, U., Stöhr, D., and Patarroyo, P. C. 1994. Erste Ergebnisse biostratigraphischer und lithstratigraphischer Untersuchungen and kretazischen Schwarzschiefern in Villa de Leiva, Boyacá, Kolumbien. *Giessener Geologische Schriften*, 51: 149–164.

Manning, R. B., and Holthuis, L. B. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). *Proceedings of the Biological Society of Washington*, 102(1): 50–77.

Manning, R. B., and Chace, F. A. 1990. Decapod and stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*, 503: 1–9.

Mantell, G. A. 1844. The Medals of Creation; First Lessons in Geology, and in the Study of Organic Remains. Bohn, London.

Marquez, F. P. L., Pohle, G. W., and Vrbora, L. 2003. On the larval stages of *Macrocoeloma diplacanthum* (Decapoda: Brachyura: Majidae), and a review of Mithracinae phylogenetic aspects. *Journal of Crustacean Biology*, 23(1): 187–200.

Marshall, C. R. 2006. Fossil record reveals tropics as cradle and museum. *Science*, 314(5796): 66–67.

Marshall, N. J., and Diebel, C. 1999. 'Deep-sea spiders' that walk through the water. *Journal of Experimental Biology*, 198(1371–1379).

Martens, E. v. 1872. Ueber Cubanische Crustaceen nach den Sammlungen Dr. J. Grundlach's. *Archiv fur Naturgeschichte*, 38: 77–147, 257, 258.

Martin, A., Serano, J. M., Jarvis, E., S., B. H., Wang, J., Ray, S., Barker, C. A., O'Connell, L. C., and Patel, N. H. 2016. CRISPR/Cas9 mutagenesis reveals versatile roles of Hox genes in crustacean limb specification and evolution. *Current Biology*, 26: 14–26.

Martin, J., and Felgenhauer, B. E. 1986. Grooming behaviour and the morphology of grooming appendages in the endemic South American crab genus *Aegla* (Decapoda, Anomura, Aeglidae). *Journal of Zoology (London)*, 209: 213–224.

Martin, J. W. 1990. Crabs of the family Homolodromiidae, II. *Dicranodromia felderi*, new species, from the Western Atlantic, with notes on the type series of *D. ovata* A. Milne Edwards, 1880. *Journal of Crustacean Biology*, 10(4): 708-720.

Martin, J. W., and Davis, G. E. 2001. An Updated Classification of the Recent Crustacea: Natural History Museum of Los Angeles County Los Angeles, California.

Martin, J. W. 2014. Brachyura. In Martin, J. W., Olesen, J. and Høeg, J. T. (Eds) *Atlas of Crustacean Larvae*, 295-310 pp. Baltimore. Johns Hopkings University Press.

Martin, J. W., Olesen, J., and Høeg, J. T. 2014. Atlas of crustacean larvae: JHU Press.

Martin, P., Bonier, F., and Tewksbury, J. 2007. Revisiting Jablonski (1993): Cladogenesis and range expansion explain latitudinal variation in taxonomic richness. *Journal of evolutionary biology*, 20(3): 930-936.

Martínez-Díaz, J. L., Phillips, G. E., Nyborg, T., Espinosa, B., de Araújo Távora, V., Centeno-García, E., and Vega, F. J. 2016. Lilliput effect in a retroplumid crab (Crustacea: Decapoda) across the K/Pg boundary. *Journal of South American Earth Sciences*, 69: 11–24.

Martínez-Díaz, J. L., Aguillón-Martínez, M. C., Luque, J., and Vega, F. J. 2017. Paleocene decapod crustacea from Northeastern Mexico: additions to biostratigraphy and diversity. *Journal of South American Earth Scienes*, 74: 67–82.

Martins-Neto, R. G. 1987. Primeiro registro de decápode na Formação Santana, bacia do Araripe (Cretáceo Inferior), Brasil. *Ciência e Cultura*, 39(4): 406–410.

Martins-Neto, R. G. 2001. Review of some Crustacea (Isopoda and Decapoda) from Brazilian deposits (Paleozoic, Mesozoic and Cenozoic) with descriptions of new taxa. *Acta Geologica Leopoldensia*, 24(52/53): 237–254.

Maury, C. J. 1930. O Cretaceo da Parahyba do Norte. *Ministerio da Agricultura, Industria e Commercio, Serviço Geologico e Mineralogico do Brasil, Monographia*, 8: 1–305.

McLaughlin, P. A., and Lemaitre, R. 1997. Carcinization in the Anomura-fact or fiction? I. Evidence from adult morphology. *Contributions to Zoology*, 67(2): 79–123.

McLaughlin, P. A., and Lemaitre, R. 2009. A new classification for the Pylochelidae (Decapoda: Anomura: Paguroidea) and descriptions of new taxa. *The Raffles Bulletin of Zoology*, 20: 159–231.

McLaughlin, P. A., Komai, T., Lemaitre, R., and Rahayu, D. L. 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part I – Lithodoidea, Lomisoidea and Paguroidea. *The Raffles Bulletin of Zoology*, 23: 5–107.

McLay, C. L. 1993. Crustacea Decapoda, the sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera. In Crosnier, A. (Ed) *Résultats des campagnes MUSORSTOM.* 10, 111-251 pp. Mémoires du Muséum National d'Histoire Naturelle, 156.

McLay, C. L. 1999. Crustacea Decapoda: Revision of the family Dynomenidae. In Crosnier, A. (Ed) *Résultats des campagnes MUSORSTOM.* 20, 427–569 pp. Mémoires du Muséum National d'Histoire Naturelle, 180.

McLay, C. L. 2001. A new genus and two new species of unusual dromiid crabs (Brachyura: Dromiidae) from northern Australia. *Records of the Australian Museum*, 53: 1–8.

McLay, C. L., and Ng, P. K. L. 2007. Revision of the Indo-West Pacific sponge crabs of the genus Petalomera Stimpson, 1858 (Decapoda: Brachyura: Dromiidae). *The Raffles Bulletin of Zoology*, 55(1): 107–120.

Merewether, E. A., Blackmon, P. D., and Webb, J. C. 1984. The mid-Cretaceous Frontier Formation near the Moxa Arch, southwestern Wyoming. *USGS Professional Paper*, 1290: 29.

Mertin, H. 1941. Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über verwandte Formen in der Oberkreide. *Nova Acta Leopoldina*, 10(68): 149–264.

Miers, E. J. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–1876. In Murray, J. (Ed) *Zoology. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873–76 Under the Command of Captain George S. Nares, R.N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N. Wyville Thomson, C. and J. Murray (series eds.).* 17, 1–362 pp. Edinburgh. Neill and Company.

Milne Edwards, H. 1830. Varune. Varuna. Crust. In Saint-Vincent, B. d. (Ed) *Dictionnaire Classique d'Histoire Naturelle.* 16, 511 p. Paris. Rey et Gravier & Amable Gobin et Cie.

Milne Edwards, H. 1832. Observations sur les Crustacés du genre *Mithrax*. *Magazine Zoologique, Classe 7, Crustacés*: 1–5.

Milne Edwards, H. 1834–1840. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Roret. Paris: Librairie Encyclopédique de Roret.

Milne Edwards, H. 1837. Histoire naturelle des Crustaces comprenant I'anatomie, la physiologie et la classification Roret. Paris.

Milne Edwards, H., and Lucas, H. 1843. Crustacés. In d'Orbigny, A. D. (Ed) *Voyage dans l' Amérique Méridionale (Le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833.*, 1–39 pp. Bertrand, Paris.

Milne Edwards, H. 1853. Mémoire sur la famille des Ocypodides. Suite (1). Deuxième Tribu Principale. *Annales des Sciences Naturelles, 3e série*, 20: 163–228.

Milne-Edwards, A. 1862. Monographie des crustacés fossiles de la famille des Canceriens. *Annales des Sciences Naturelles, 4e série*, 18: 31–85.

Milne-Edwards, A. 1863. Monographie des Crustacés Fossiles de la Famille des Cancériens. *Annales des Sciences Naturelles, 4e série*, 20: 273–324.

Milne-Edwards, A. 1865. Monographie des Crustacés Fossiles de la Famille des Cancériens. *Annales des Sciences Naturelles, 5e série*, 3: 297–351.

Milne-Edwards, A. 1873. Descriptions des quelques crustacés nouveaux ou peu connus provenant du Musée de M. C. Godeffroy. *Journal des Museum Godeffroy*, 1: 77–88, Plates 12–13.

Milne-Edwards, A. 1873–1880. Études sur les xiphosures et les crustacés de la région mexicaine. Mission scientifique au Mexique et dans l'Amérique centrale, ouvrage publié par ordre du Ministre de l'Instruction publique. Recherches zoologiques pour servir à l'histoire de la faune de l'Amérique centrale et du Mexique, publiées sous la direction de M.H. Milne Edwards, membre de l'Institut. Cinquième partie. Paris: Imprimerie Nationale. 8 [unnumbered].

Milne-Edwards, A. 1878. Description de quelques espèces nouvelles de Crustacés, provenant du Voyage aux îles du Cap Vert de MM. Bouvier et Cessac. *Bulletin de la Société Philomathique de Paris*, 7(2): 225–232.

Milne-Edwards, A. 1880a. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey Steamer "Blake," Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les crustacés. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 8(1): 1–68.

Milne-Edwards, A. 1880b. Études préliminaires sur les Crustacés, 1ère partie. Reports on the Results of Dredging under the Supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the U.S. Coast Guard Survey Steamer 'Blake', Lieutenant-Commander, C. D. Sigsbee, U.S.N., and Commander, J. R. Bartlett, U.S.N., Commanding. VIII. *Bulletin of the Museum of Comparative Zoology, Harvard*, 8(1): 1–68.

Milne-Edwards, A. 1881a. Description de quelques crustacés macroures provenant des grandes profondeurs de la Mer des Antilles. *Annales des Sciences Naturelles, 6e série*, 11: 1–15.

Milne-Edwards, A. 1881b. Note sur quelques crustacés fossiles des environs de Biarritz. *Annales des Sciences Géologiques*, 11: 1–8, Plates 21–22.

Milne-Edwards, A., and Bouvier, E. L. 1893. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U. S. Coast Survey steamer "Blake," Lieut-Com. S. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., commanding. XXXIII. Description des Crustacés de la famille des paguriens recueillis pendant l'expédition. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 14(3): 5–172, Plates I–XII.

Milne-Edwards, A., and Bouvier, E. L. 1923. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of México (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic Coast of the United States (1880), by the U.S. Coast Steamer 'Blake', Lieutenant-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding, XLVII. Les Porcellanidés et les Brachyures. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 47: 281–395.

Minagawa, M. 1990. Complete larval development of the red frog crab *Ranina ranina* (Crustacea, Decapoda, Raninidae) reared in the laboratory. *Nippon Suisan Gakkaishi*, 56(4): 577-589.

Minh, B. Q., Nguyen, M. A. T., and von Haeseler, A. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30(5): 1188-1195.

Monod, T. 1956. Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut Français d'Afrique Noire*, 45: 1–674.

Moody, J. M., and Maisey, J. G. 1994. New Cretaceous marine vertebrate assemblages from North-Western Venezuela and their significance. *Journal of Vertebrate Paleontology*, 14(1): 1-8.

Morales, L. G., Podesta, D. J., Hatfield, W. C., Tanner, H., Jones, S. H., Barker, M. H., O'Donoghue, D. J., Mohler, C. E., Dubois, E. P., Jacobs, C., and Goss, C. R. 1958. General geology and oil occurrence of the Middle Magdalena Valley, Colombia. In Weeks, L. G. (Ed) *Habitat of Oil: A Symposium*, 641–695 pp. Tulsa, Oklahoma, USA. American Association of Petroleum Geologists.

Moreno, G., and Sarmiento, G. 2002. Estratigrafía Cuantitativa de las Formaciones Tablazo y Simití en las localidades de Sáchica (Boyacá) y Barichara – San Gil (Santander), Colombia. *Geología Colombiana*, 27: 51–76.

Morris, S. F. 1973. Guide to the Geology of the Cuenca Basin, Southern Ecuador. In Bristow, C. R. (Ed) *Ecuadorian Geological and Geophysical Society*, 54 p. Quito.

Morris, S. F. 1993. The fossil arthropods of Jamaica. In Wright, R. M. and Robinson, E. (Eds) *Biostratigraphy of Jamaica. Geological Society of America Memoirs.* 182, 115–124 pp.

Müller, P. 1984. Decapod Crustacea of the Badenian. *Institutum Geologicicum Hungaricum, Geologica Hungarica, Series Palaeontologica*, 42: 3–317.

Negreiros-Fransozo, M. L., Wenner, E. L., Knott, D. M., and Fransozo, A. 2007. The megalopa and early juvenile stages of *Calappa tortugae* Rathbun, 1933 (Crustacea, Brachyura) reared in the laboratory from South Carolina neuston samples. *Proceedings of the Biological Society of Washington*, 120(4): 469–485.

Negreiros-Fransozo, M. L., Fernandes, C. S., Januário Da Silva, S. M., and Fransozo, A. 2011. Early juvenile development of *Armases rubripes* (Rathbun 1897) (Crustacea, Brachyura, Sesarmidae) and comments on the morphology of the megalopa and first crab. *Invertebrate reproduction and development*, 55(1): 53–64.

Newman, W. A. 1983. Origin of the Maxillopoda; urmalacostracan ontogeny and progenesis. *Crustacean Issues*, 1: 105–119.

Ng, P. K. L., and Rodríguez, G. 1986. New records of *Mimilambrus wileyi* Williams, 1979 (Crustacea: Decapoda: Brachyura), with notes on the systematics of the Mimilambridae Williams, 1979 and

Parthenopoidea MacLeay, 1838 sensu Guinot, 1978. *Proceedings of the Biological Society of Washington*, 99: 88–99.

Ng, P. K. L., and Holthuis, L. B. 2007. Case 3394. *Etisus* H. Milne Edwards, 1834 and *Chlorodiella* Rathbun, 1897 (Crustacea, Decapoda, Brachyura): Proposed conservation of the generic names by suppression of the generic name *Clorodius* A. G. Desmarest, 1823. *Bulletin of Zoological Nomenclature*, 64(1): 19–24.

Ng, P. K. L., Guinot, D., and Davie, P. J. F. 2008. Systema Brachyurorum: Part I. An Annotated Checklist of Extant Brachyuran Crabs of the World. *The Raffles Bulletin of Zoology*, 17: 1–186.

Nguyen, L.-T., Schmidt, H. A., von Haeseler, A., and Minh, B. Q. 2015. IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Molecular Biology and Evolution*, 32(1): 268-274.

Nilsson, D.-E. 1990a. Three unexpected cases of refracting superposition eyes in crustaceans. *J Comp Physiol A*, 167.

Nilsson, D. E. 1983. Evolutionary links between apposition and superposition optics in crustacean eyes. *Nature*, 302(5911): 818-821.

Nilsson, D. E., Hallberg, E., and Elofsson, R. 1986. The ontogenetic development of refracting superposition eyes in crustaceans: Transformation of optical design. *Tissue and Cell*, 18(4): 509-519.

Nilsson, D. E. 1988. A new type of imaging optics in compound eyes. *Nature*, 332(6159): 76–78.

Nilsson, D. E. 1989. Optics and evolution in the compound eye. In Stavenga, D. G. and Hardie, R. C. (Eds) *Facets of vision*. Berlin. Springer.

Nilsson, D. E. 1990b. Three unexpected cases of refracting superposition eyes in crustaceans. *Journal of Comparative Physiology A*, 167: 71–78.

Norse, E. A., and Fox-Norse, V. 1977. Studies on portunid crabs from the Eastern PAcific. II. Significance of the unusual distribution of *Euphylax dovii*. *Marine Biology*, 40: 374–376.

O'Reilly, J. E., Puttick, M. N., Parry, L., Tanner, A. R., Tarver, J. E., Fleming, J., Pisani, D., and Donoghue, P. C. J. 2016. Bayesian methods outperform parsimony but at the expense of precision in the estimation of phylogeny from discrete morphological data. *Biology Letters*, 12(4).

Orbigny, A. D. d. 1842. Voyage dans l'Amérique méridional, 1826-1833. Géologie et Paléontologie. Paris.

Ordway, A. 1863. Monograph of the genus *Callinectes*. *Journal of the Boston Society of Natural History*, 7: 567–583.

Ortmann, A. E. 1892a. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. IV. Die Abtheilungen Galatheidea und Paguridea.*Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere.* 6, 241–326 pp.

Ortmann, A. E. 1892b. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. V Theil. Die Abtheilungen Hippidea, Dromiidea und Oxystomata*Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere.* 6, 532–588 pp.

Ortmann, A. E. 1893. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VII. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Zoologische Jahrbücher. *Abteilung für Systematik, Geographie und Biologie der Thiere*, 7(3): 411–495.

Ortmann, A. E. 1898. Crustacea, Malacostraca. In Gerstäcker, A. and Ortmann, A. E. (Eds) *Die Klassen und Ordnungen der Arthropoden wissenschaftlich dargestellt in Wort und Bild, in H.G. Bronn's*

Die Klassen und Ordnungen der Thier-Reichs wissenschaftlich dargestellt in Wort und Bild. 5 (2). Leipzig. Winter'sche Verlagshandlung.

Osawa, M., and McLaughlin, P. A. 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part II – Porcellanidae. *The Raffles Bulletin of Zoology*, 23: 109–129.

Ossó, À., Domínguez, J. L., and Artal, P. 2014. *Pyreneplax basaensis* new genus, new species (Decapoda, Brachyura, Vultocinidae) from the Priabonian (Late Eocene) of the Pyrenees of Huesca (Aragón, Spain), and remarks on the genus *Lobonotus* A. Milne-Edwards, 1863. *Treballs del Museu de Zoologia, Barcelona*, 20: 33–43.

Páramo, M. 1997. *Platypterigius sachicarum* (Reptilia, Ichthyosauria) Nueva Especie del Cretácico de Colombia. *Revista INGEOMINAS*, 6: 1–12.

Pasini, G., and Garassino, A. 2017. A preliminary review of the fossil species of *Ranina* Lamarck, 1801(Decapoda, Brachyura, Raninidae), with systematic remarks. *Natural History Sciences. Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, 4(1): 43–72.

Patarroyo, P. C. 2000. Distribución de amonitas del Barremiano de la Formación Paja en el sector de Villa de Leiva (Boyacá, Colombia). Bioestratigrafía. *Geología COlombiana*, 25: 149–162.

Patrulius, D. 1959. Contributions à la systématique des Décapodes néojurassiques. *Revue de Géologie et Géographie*, 3(2)(249–257).

Paul'son, O. 1875. Studies on the Crustacea of the Red Sea with notes regarding other seas. Part 1. Podophthalmata and Edriophthalmata (Cumacea), 1–164 pp. (S. V. Kul'zhenko, Kiev). [Translation published for The National Science Foundation,Washington, D.C. and Smithsonian Institution, U.S.A., by the Israel Program for Scientific Translations, 1961].

Peñalver, L. L., Lavandero, R., and Barriendo, A. 1997. Sistema cuaternario. In Furrazola-Bermúdez, G. and Núñez-Cambra, K. (Eds) *Estudios sobre Geología de Cuba*, 165–178 pp. La Habana. Instituto Geológico y Paleontológico.

Philippi, R. A. 1887. Die Tertiären und Quartáren Versteinerunge Chiles. Brockhaus, Leipzig.

Phillips, G. E., Nyborg, T., and Vega, F. J. 2014. Icriocarcinidae: A family of portunoid crabs from the Upper Cretaceous of North America. *Paläontologische Zeitschrift*, 88: 139–158.

Plotnick, R. E. 1985. Lift based mechanisms for swimming in eurypterids and portunid crabs. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 76(2–3): 325–337.

Pons, D., Berthou, P. Y., and Campos, D. A. 1990. Quelques observations sur la palynologie de l'Aptien Superieur et de l'Albien du bassin d'Araripe (NE du Bresil). *Atas do 1 Simposio Bacia do Araripe 1990*: 241-252.

Portell, R. W., and Schindler, K. S. 1991. *Menippe mercenaria* (Decapoda: Xanthidae) from the Pleistocene of Florida. *Papers in Florida Paleontology*, 3: 1–8.

Portell, R. W., and Collins, J. S. H. 2002. A new species of *Montezumella* (Crustacea: Decapoda: Cheiragonidae) from the upper Eocene Ocala Limestone of Florida. *Proceedings of the Biological Society of Washington*, 115(3): 594–599.

Portell, R. W., Turner, R. L., and Beerensson, J. L. 2003. Occurrence of the Atlantic ghost crab *Ocypode quadrata* from the upper Pleistocene to Holocene Anastasia Formation of Florida. *Journal of Crustacean Biology*, 23(3): 712–722.

Portell, R. W. 2004. Eocene, Oligocene, and Miocene decapod crustaceans. *Florida Fossil Invertebrates*, 5: 1–28.

Portell, R. W., and Agnew, J. 2004. Pliocene and Pleistocene decapod crustaceans. *Florida Fossil Invertebrates*, 4: 1–29.

Portell, R. W., and Collins, J. S. H. 2004. Decapod crustaceans of the lower Miocene Montpelier Formation, White Limestone Group of Jamaica. *Cainozoic Research*, 3(1-2): 109–126.

Portell, R. W., Luque, J., Hendy, A. J. W., and Christy, J. H. 2012. Fidelity of marine invertebrate death and fossil assemblages in a coastal marine ecosystem, Bahia Bique, Panama. Geological Society of America Annual Meeting, Abstracts with Programs, 44(7): 268.

Porter, M. L., and Cronin, T. W. 2009. A shrimp's eye view of evolution: How useful are visual characters in decapod phylogenetics? In Martin, J. W., Crandall, K. A. and Felder, D. L. (Eds) *Decapod Crustacean Phylogenetics: Crustacean Issues.* 18, 183–195 pp.

Prado, L. A. C., Luque, J., Barreto, A. M. F., and Palmer, A. R. submitted. New orithopsid crabs (Decapoda: Brachyura: Raninoida) from the Aptian–Albian Romualdo Formation, Santana Group of Brazil: evidence for a tethyan connection to the Araripe Basin. *Acta Palaeontologica Polonica*.

Pretzmann, G. 1968. Die Familie Trichodactylidae (Milne Edwards, 1853) Smith (vorläufige Mitteilung). *Entomologisches Nachrichtenblatt*, 15: 70–76.

Pretzmann, G. 1978. Neue Süßwasserkrabben aus den Anden. *Sitzungsberichten der Österreichischen Akademie der Wissenschaften, (Mathematisch-naturwissenschaftliche Klasse) (1)*, 187(6-10): 163–170.

Pulido, O. 1979. Geología de las Planchas 135 San Gil y 151 Charalá; Departamento de Santander. *Boletín Geológico del Ministerio de Minas y Energía, Instituto Nacional Investigaciones Geológicas y Minerales*, 23(2): 61.

Pulido, O. 1985. Geología de la Plancha 135 San Gil, Escala 1:100000. Bogotá: Instituto Colombiano de Geología y Minería INGEOMINAS.

Rafinesque, C. S. 1815. Analyse de la Nature, ou Tableau de l'Univers et des Corps Organisés. Palermo, Italy: L'Imprimerie de Jean Barravecchia.

Rambaut, A., Suchard, M. A., Xie, D., and Drummond, A. J. Tracer v1.6, Available from http://beast.bio.ed.ac.uk/Tracer

Randall, J. W. 1840. Catalogue of the Crustacea brought by Thomas Nuttall and J. K. Townsend, from the west coast of North America and the Sandwich Islands, with descriptions of such species as are apparently new, among which are included several species of different localities, previously existing in the collection of the Academy. *Journal of the Academy of Natural Sciences of Philadelphia*, 8(1): 106–147.

Rathbun, M. J. 1892. Catalogue of the crabs of the family Periceridae in the U.S. National Museum. *Proceedings of the United States National Museum*, 15: 231–277.

Rathbun, M. J. 1893. Scientific results of explorations by the U.S. Fish Commission steamer Albatross. No. XXIV.—Descriptions of new genera and species of crabs from the west coast of North America and the Sandwich Islands. *Proceedings of the United States National Museum*, 16(933): 223–260.

Rathbun, M. J. 1896. The genus *Callinectes*. *Proceedings of the United States National Museum*, 18(1070): 349–375.

Rathbun, M. J. 1897a. A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society of Washington*, 11: 153–167.

Rathbun, M. J. 1897b. List of the decapod Crustacea of Jamaica. *Annals of the Institute of Jamaica*, 1(1): 3–46.

Rathbun, M. J. 1898. The Brachyura of the biological expedition to the Florida Keys and the Bahamas in 1893. *Bulletin from the Laboratories of Natural History, State University of Iowa*, 4(3): 250–294.

Rathbun, M. J. 1902. Descriptions of new decapod crustaceans from the west coast of North America. *Proceedings of the U. S. National Museum*, 24: 885–905.

Rathbun, M. J. 1904. Some changes in crustacean nomenclature. *Proceedings of the Biological Society of Washington*, 17: 169–172.

Rathbun, M. J. 1908. Descriptions of fossil crabs from California. *Proceedings of the United States National Museum*, 35: 341–349.

Rathbun, M. J. 1917. New species of South Dakota Cretaceous crabs. *Proceedings of the United States National Museum*, 52: 385–391.

Rathbun, M. J. 1918 [1919]. Decapod crustaceans from the Panama region. In Vaughan, T. W. (Ed) *Contributions to the geology and paleontology of the Canal Zone, Panama and geologically* *related areas in Central America and the West Indies. Bulletin of the United States National Museum.* 103, 123–184 pp.

Rathbun, M. J. 1919. West Indian Tertiary decapod crustaceans. *Publications of the Carnegie Institution*, 291: 157–184.

Rathbun, M. J. 1920a. New species of spider crabs from the Straits of Florida and Caribbean Sea. *Proceedings of the Biological Society of Washington*, 33: 23–24.

Rathbun, M. J. 1920b. Additions to the West Indian Tertiary decapod crustaceans. *Proceedings of the United States National Museum*, 58: 381–384.

Rathbun, M. J. 1923a. Decapod crustaceans from the Upper Cretaceous of North Carolina. In Stephenson, L. W. (Ed) *The Cretaceous formations of North Carolina*, 403–408 pp. Raleigh. North Carolina Geological Survey.

Rathbun, M. J. 1923b. Fossil crabs from the Republic of Haiti. *Proceedings of the Biological Society of Washington*, 63: 1–6.

Rathbun, M. J. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America: US Government Printing Office.

Rathbun, M. J. 1928. Two new crabs from the Eocene of Texas. *Proceedings of the United States National Museum*, 73: 1–6.

Rathbun, M. J. 1929. A new crab from the Eocene of Florida. *Proceedings of the United States National Museum*, 75: 1–4.

Rathbun, M. J. 1930. Fossil decapod crustaceans from Mexico. *Proceedings of the United States National Museum*, 78: 1–10.

Rathbun, M. J. 1931. Two new crabs from the Gulf of Mexico. *Proceedings of the Biological Society of Washington*, 44: 71–72.

Rathbun, M. J. 1933. Preliminary descriptions of nine new species of oxystomatous and allied crabs. *Proceedings of the Biological Society of Washington*, 46: 183–186.

Rathbun, M. J. 1935a. Preliminary descriptions of seven new species of oxystomatous and allied crabs. *Proceedings of the Biological Society of Washington*, 48: 1–4.

Rathbun, M. J. 1935b. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America*, Special Paper(2): i–viii, 1–160.

Rathbun, M. J. 1937. Cretaceous and Tertiary crabs from Panama and Colombia. *Journal of Paleontology*, 11(1): 26–28.

Reese, E. S., and Kinzie, R. A., III. 1968. The larval development of the coconut or robber crab *Birgus latro* (L.) in the laboratory (Anomura, Paguridea). *Crustaceana Supplement*(2): 117–144.

Rice, A. L., and Ingle, R. W. 1977. "Ship-Wrecked" raninid and portunid crab larvae from the South-Western Indian Ocean (Decapoda, Brachyura). *Crustaceana*, 32(1): 94-97.

Richards, B. C. 1975. *Longusorbis cuniculosus*: A new genus and species of Upper Cretaceous crab with comments on the Spray Formation at Shelter Point, Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences*, 12: 1850–1863.

Richards, H. G. 1935. Pleistocene mollusks from western Cuba. *Journal of Paleontology*, 9(3): 253–258.

Roberts, H. B. 1962. The Upper Cretaceous decapod crustaceans of New Jersey and Delaware. In Richards, H. G. (Ed) *The Cretaceous Fossils of New Jersey.* Bulletin 61, 163–191 pp. New Jersey Bureau of Geology and Topography.

Roberts, T. R. 1975. Characoid fish teeth from Miocene deposits in the Cuenca Basin, Ecuador. *Journal of Zoology*, 175(2): 259–271.

Robins, C. M., Freierman, A., O'Neill, J., Pearson, L., Luque, J., and Portell, R. W. 2016. Sexual dimorphism and ontogeny within the fossil brachyuran crabs *Falconoplax* (Chasmocarcinidae) and *Palaeopinnixa* (Hexapodidae) from the lower Miocene Culebra Formation of Panama.*6th Symposium on Cretaceous and Cenozoic Decapod Crustaceans (June 14–18)* (p. 62). Villers-sur-Mer, Normandy, France.

Rodriguez, G. 1997. Trichodactylid crabs. In Kay, R. F., Madden, R. H., Cifelly, R. L. and Flynn, J. J. (Eds) *Vertebrate paleontology in the Neotropics. The Miocene fauna of La Venta, Colombia*, 63–66 pp. Washington, D.C. Smithsonian Institution Press.

Roemer, F. A. 1887. *Graptocarcinus texanus*, ein Brachyure aus der oberen Kreide von Texas. *Leonhardt und Bronn's Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, 1: 173–176.

Romanov, E., Potier, M., Zamorov, V., and Ménard, F. 2009. The swimming crab *Charybdis smithii*: distribution, biology and trophic role in the pelagic ecosystem of the western Indian Ocean. *Marine Biology*, 156: 1089–1107.

Ronquist, F., van der Mark, P., and Huelsenbeck, J. P. 2009. Bayesian phylogenetic analysis using MrBayes. In Lemey, P., Salemi, M. and Vandamme, A.-M. (Eds) *The phylogenetic handbook*. Cambridge. Cambridge University Press.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3): 539-542.

Ross, A., Lewis, J. E., and Scolaro, R. J. 1964. New Eocene decapods from Florida. *Quarterly Journal of the Florida Academy of Sciences*, 27(4): 187–196.

Ross, A., and Scolaro, R. J. 1964. A new crab from the Eocene of Florida. *Quarterly Journal of the Florida Academy of Sciences*, 27: 97–106.

Rumphus, G. E. 1705. D'Amboinsche Rariteitkamer. Behelzende eene Beschryvinge van allerhande zoo weeke als harde Schaalvisschen, te weeten raare Krabben, Kreeften, en diergelyke Zeedieren, als mede allerhande Hoorntjes en Schulpen, die men in d'Amboinsche Zee vindt: Daar beneven sommige Mineraalen, Gesteenten, en soorten van Aarde, die in d'Amboinsche, en zommige omleggende Eilanden gevonden worden. Verdeelt in drie Boeken, En met nodige Printverbeeldingen, alle naar't leven getekent, voorzien. T'Amsterdam. Gedrukt by François Halma, Boekverkoper in Konstantijn den Grooten. F. Halma, Amsterdan. Vol. XXVII: + 340 pp.

Rumsey, B. T., Klompmaker, A. A., and Portell, R. W. 2016. Paleobiogeography of the fossil box crab *Calappilia* (Brachyura: Calappidae) with a new species from the Eocene-Oligocene of Florida, USA. *Journal of Crustacean Biology*, 36(3): 329–337.

Saint Laurent, M. d. 1980. Sur la classification et la phylogénie des Crustacés Décapodes Brachyoures. I. Podotremata Guinot, 1977 et Eubrachyura sect. nov. *Comptes rendus hebdomadaires des séances de l'Académie des sciences*, série III(290): 1265–1268.

Samouelle, G. 1819. The entomologist's useful compendium; or an introduction to the knowledge of British insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and the modern method of arranging the classes Crustacea, Myriapoda, Spiders, Mites and Insects, from their affinities and structure, according to the views of Dr. Leach. London.

Sánchez-Quiñonez, C., and Tchegliakova, N. 2005. Foraminíferos planctónicos de la Formación San Rafael, Cretácico Superior, en los alrededores de Villa de Leiva, Boyacá, Colombia. *Geología Colombiana*, 30: 99–126.

Saussure, H. d. 1853. Description de quelques crustacés nouveaux de la côte occidentale du Mexique. *Revue et Magasin de Zoologie (série 2)*, 5: 354–368.

Saussure, H. d. 1858. Mémoire sur divers Crustacés nouveaux de Mexique et des Antilles. *Mémoires, Société Physique et d'Histoire Naturelle de Genéve*, 14(2): 417–496.

Say, T. 1817–1818. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, 1 (1) [1817]: 57–63, 65–80, 97–101, 155–169; (2) [1818]: 235–253, 313–319, 374–401, 423–444, 445–458.

Scholtz, G., and Richter, S. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnaean Society*, 113: 289–328.

Scholtz, G., and McLay, C. L. 2009. Is the Brachyura Podotremata a monophyletic group? In Martin, J. W., Crandall, K. A. and Felder, D. L. (Eds) *Decapod Crustacean Phylogenetics. Crustacean Issues.* 18, 417–435 pp.

Scholtz, G. 2014. Evolution of crabs–history and deconstruction of a prime example of convergence. *Contributions to Zoology*, 83(2): 87–105.

Schram, F. R., Feldmann, R. M., and Copeland, M. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. *Journal of Paleontology*, 52(6): 1375-1387.

Schram, F. R. 1986. Crustacea: Oxford University Press, New York.

Schram, F. R., and Koenemann, S. 2004. Developmental genetics and arthropod evolution: On body regions of Crustacea. In Schram, F. R. (Ed) *Evolutionary Developmental Biology of Crustacea, Crustacean Issues 15:*, 75–92 pp. Balkema, Lisse.

Schultze, H. P., and Stöhr, D. 1996. Vinctifer (Pisces, Aspidorynchidae) aus der Unterkreide (oberes Aptium) von Kolumbien. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 199(3): 395–415.

Schweigert, G., and Koppka, J. 2011. Decapods (Crustacea: Brachyura) from the Jurassic of Germany and Lithuania, with descriptions of new species of *Planoprosopon* and *Tanidromites*. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 260(2): 221–235.

Schweitzer, C. E., and Feldmann, R. M. 2000. Reevaluation of the Cancridae Latreille, 1803 (Decapoda: Brachyura) including three new genera and three new species. *Contributions to Zoology*, 69: 223–250.

Schweitzer, C. E. 2001. Paleobiogeography of Cretaceous and Tertiary Decapod Crustaceans of the North Pacific Ocean. *Journal of Paleontology*, 75(4): 808-826.

Schweitzer, C. E., and Feldmann, R. M. 2001. Differentiation of the fossil Hexapodidae Miers, 1886 (Decapoda: Brachyura) from similar forms. *Journal of Paleontology*, 75: 330–345.

Schweitzer, C. E., and Feldmann, R. M. 2002. New Eocene decapods (Thalassinidea and Brachyura) from Southern California. *Journal of Crustacean Biology*, 22(4): 938–967.

Schweitzer, C. E., Feldmann, R. M., González–Barba, G., and Vega, F. J. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic Implications of Mexican fossil decapods. *Paleontological Society Memoir*, 76: 1–43.

Schweitzer, C. E. 2003. Utility of proxy characters for classification of fossils: an example from the fossil Xanthoidea (Crustacea: Decapoda: Brachyura). *Journal of Paleontology*, 77(6): 1107–1128.

Schweitzer, C. E., Feldmann, R. M., Fam, J., Hessin, W. A., Hetrick, S. W., Nyborg, T. G., and Ross, R. L. M. 2003a. Cretaceous and Eocene Decapod Crustaceans from Southern Vancouver Island, British Columbia, Canada. Ottawa, Ontario: NRC Research Press.

Schweitzer, C. E., Lacovara, K. J., Smith, J. B., Lamanna, M. C., Lyon, M. A., and Attia, Y. 2003b. Mangrove-dwelling crabs (Decapoda: Brachyura: Necrocarcinidae) associated with dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. *Journal of Paleontology*, 77(5): 888–894.

Schweitzer, C. E. 2005a. The Trapeziidae and Domeciidae (Decapoda: Brachyura: Xanthoidea) in the fossil record and a new Eocene genus from Baja California Sur, Mexico. *Journal of Crustacean Biology*, 25(4): 625–636.

Schweitzer, C. E. 2005b. The genus *Xanthilites* Bell, 1858 and a new xanthoid family (Crustacea: Decapoda: Brachyura: Xanthoidea): New hypotheses on the origin of the Xanthoidea MacLeay, 1838. *Journal of Paleontology*, 79: 277–295.

Schweitzer, C. E., González-Barba, G., Feldmann, R. M., and Waugh, D. A. 2005. Decapoda (Thalassinidea and Paguroidea) from the Eocene Bateque and Tepetate Formations, Baja California Sur, Mexico: systematics, cuticle microstructure, and paleoecology. *Annals of Carnegie Museum*, 74(4): 275–293.

Schweitzer, C. E., Feldmann, R. M., Encinas, A., and Súarez, M. 2006a. New Cretaceous and Eocene Callianassoidea (Thalassinidea, Decapoda) from Algarrobo, Chile. *Journal of Crustacean Biology*, 26(1): 73–81.

Schweitzer, C. E., Feldmann, R. M., González-Barba, G., and Cosovic, V. 2006b. New Decapoda (Anomura, Brachyura) from the Eocene Bateque and Tepetate Formations, Baja California Sur, Mexico. *Bulletin of the Mizunami Fossil Museum*, 33: 21–45.

Schweitzer, C. E., Iturralde–Vinent, M., Hetler, J. L., and Velez–Juarbe, J. 2006c. Oligocene and Miocene decapods (Thalassinidea and Brachyura) from the Caribbean. *Annals of Carnegie Museum*, 75(2): 111–136.

Schweitzer, C. E., Artal, P., van Bakel, B., Jagt, J. W., and Karasawa, H. 2007a. Revision of the genus *Titanocarcinus* (Decapoda: Brachyura: Xanthoidea) with two new genera and one new species. *Journal of Crustacean Biology*, 27(2): 278–295.

Schweitzer, C. E., Feldmann, R. M., González-Barba, G., and Ćosović, V. 2007b. Decapod crustaceans (Brachyura) form the Eocene Tepetate Formation, Baja California Sur, Mexico. *Annals of Carnegie Museum*, 76(1): 1–14.

Schweitzer, C. E., Feldmann, R. M., and Karasawa, H. 2007c. Revision of the Carcineretidae Beurlen, 1930 (Decapoda: Brachyura: Portunoidea) and remarks on the Portunidae Rafinesque, 1815. *Annals of Carnegie Museum*, 76(1): 15–37.

Schweitzer, C. E., Velez-Juarbe, J., Martinez, M., Collmar Hull, A., Feldmann, R. M., and Santos, H. 2008. New Cretaceous and Cenozoic Decapoda (Crustacea: Thalassinidea, Brachyura) from Puerto Rico, United States Territory. *Bulletin of the Mizunami Fossil Museum*, 34: 1–15.

Schweitzer, C. E., and Feldmann, R. M. 2009. Revision of the Prosopinae sensu Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species. *Annalen des Naturhistorischen Museums in Wien*, 110(A): 55–121.

Schweitzer, C. E., and Feldmann, R. M. 2010a. Sphaerodromiidae (Brachyura: Dromiacea: Dromioidea) in the Fossil Record. *Journal of Crustacean Biology*, 30(3): 417–429.

Schweitzer, C. E., and Feldmann, R. M. 2010b. The Decapoda (Crustacea) as predators on Mollusca through geologic time. *Palaios*, 25(167–182).

Schweitzer, C. E., and Feldmann, R. M. 2010c. The oldest Brachyura (Decapoda: Homolodromioidea: Glaessneropsoidea) known to date (Jurassic). *Journal of Crustacean Biology*, 30(2): 251–256.

Schweitzer, C. E., Feldmann, R. M., Garassino, A., Karasawa, H., and Schweigert, G. 2010. Systematic List of Fossil Decapod Crustacean Species. Leiden: Brill.

Schweitzer, C. E., Dworschak, P. C., and Martin, J. W. 2011. Replacement names for several fossil Decapoda. *Journal of Crustacean Biology*, 31(2): 361–363.

Schweitzer, C. E., and Feldmann, R. M. 2011a. Revision of some fossil podotrematous Brachyura (Homolodromiidae; Longodromitidae; Torynommidae). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 260(2): 237–256.

Schweitzer, C. E., and Feldmann, R. M. 2011b. New fossil Brachyura (Decapoda: Homoloidea, Dorippoidea, Carpilioidea) from the United Kingdom. *Bulletin of the Mizunami Fossil Museum*, 37: 1–11.

Schweitzer, C. E., and Feldmann, R. M. 2012. Revision of Decapoda deposited in The Muséum national d'Histoire naturelle, Paris. *Bulletin of the Mizunami Fossil Museum*, 38: 15–27.

Schweitzer, C. E., and Feldmann, R. M. 2015. Faunal turnover and niche stability in marine Decapoda in the Phanerozoic. *Journal of Crustacean Biology*, 35(5): 633–649.

Schweitzer, C. E., Karasawa, H., Luque, J., and Feldmann, R. M. 2016. Phylogeny and classification of Necrocarcinoidea Förster, 1968 (Brachyura: Raninoida) with description of two new genera. *Journal of Crustacean Biology*, 36(3): 338–372.

Secretan, S. 1972. Crustacés Décapodes nouveaux du Crétacé supérieur de Bolivie. *Bulletin du Muséum National d'Histoire Naturelle, third series*, 49: 1–15.

Serène, R. 1964. Redescription du genre *Megaesthesius* Rathbun et dèfinition de Chasmocarcininae, nouvelle sous-famille des Goneplacidae (Decapoda Brachyura). *Crustaceana*, 7(3): 175–187.

Serène, R. 1965. Guide for curators of brachyuran collections in Southeast Asia. *Bangkok: Applied Scientific Research Corporation of Thailand*: 65 pp.

Serène, R., and Umali, F. 1972. The family Raninidae and other new and rare species of brachyuran decapods from the Philippines and adjacent regions. *The Philippine Journal of Science*, 99(1–2): 21–105.

Serrano-Sánchez, M. d. L., Guerao, G., Centeno-García, E., and Vega, F. J. 2016. Crabs (Brachyura: Grapsoidea: Sesarmidae) as inclusions in Lower Miocene amber from Chiapas, Mexico. *Boletín de la Sociedad Geológica Mexicana*, 68(1): 37–43.

Skilleter, G. A., and Anderson, D. T. 1986. Functional morphology of the chelipeds, mouthparts and gastric mill of *Ozius truncatus* (Milne Edwards) (Xanthidae) and *Leptograpsus variegatus* (Fabricius) (Grapsidae) (Brachyura). *Australian Journal of Marine and Freshwater Research*, 37: 67–79.

Skinner, D. G., and Hill, B. J. 1986. Catch rate and emergence of male and female spanner crabs (*Ranina ranina*) in Australia. *Marine Biology*, 91: 461–465.

Smith, S. I. 1869a. Notice of the Crustacea collected by Prof. C. F. Hartt on the coast of Brazil in 1867, list of the described species of Brazilian Podophthalmia. *Transactions of the Connecticut Academy of Arts and Sciences*, 2: 1–41.

Smith, S. I. 1869b. On the parasitic habits of Crustacea. In Verrill, A. E. (Ed) *American Naturalist.* 3, 239–250 pp.

Smith, S. I. 1870. Notes on American Crustacea. No. 1. Ocypodoidea. *Transactions of the Connecticut Academy of Arts and Science*, 2: 113–176.

Soares, M. d. O., Xerez Barrosoa, C., Soares Lima, Í. C. C., Santiago, M. M. F., and Lemos, V. B. 2016. Holocene invertebrates from the Rocas Atoll: A contribution for the ecological history of South Atlantic islands. *Journal of Integrated Coastal Zone Management*, 16(1): 89–94.

Spears, T., Abele, L. G., and Kim, W. 1992. The Monophyly of Brachyuran Crabs: A Phylogenetic Study Based on 18s rRNA. *Systematic Biology*, 41(4): 446–461.

Spiridonov, V. A., Neretina, T. V., and Schepetov, D. 2014. Morphological characterization and molecular phylogeny of Portunoidea Rafinesque, 1815 (Crustacea Brachyura): implications for understanding evolution of swimming capacity and revision of the family-level classification. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 253(5): 404–429.

Squires, R. L., and Demetrion, R. A. 1992. Paleontology of the Eocene Bateque Formation, Baja California Sur, Mexico. *Natural History Museum of Los Angeles County Contributions in Science*, 434: 1–55.

Stenzel, H. B. 1944a. A new Cretaceous crab, *Graptocarcinus muiri*, from Mexico. *Journal of Paleontology*, 18(6): 550–552.

Stenzel, H. B. 1944b. A new Paleocene catometope crab from Texas, *Tehuacana tehuacana*. *Journal of Paleontology*, 18: 546–549.

Stenzel, H. B. 1945. Decapod crustaceans from the Cretaceous of Texas. *The University of Texas Publication*, 4401: 401-477.

Stephenson, W., and Campbell, B. 1960. The Australian portunids (Crustacea: Portunidae). IV. Remaining genera. *Marine and Freshwater Research*, 11(1): 73–122.

Stepp, A. M. 2014. Descriptions and biodiversity of decapods in the Seroe Domi Formation of Curaçao; Masters of Science thesis (p. 80). Ohio, USA: Kent State University.

Števčić, Z. 1973. The systematic position of the family Raninidae. *Systematic Zoology*(22): 625-632.

Števčić, Z. 1983. Revision of the Calappidae. *Memoirs of the Australian Museum*, 18: 165–171.

Števčić, Z. 1995. Brachyuran systematics and the position of the family Raninidae reconsidered. *Arthropoda Selecta*, 4: 27-36.

Števčić, Z. 2005. The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica*, 14(1): 1–159.

Stimpson, W. 1857. Notices of new species of Crustacea of western North America; being an abstract from a paper to be published in the journal of the Society. *Proceedings of the Boston Society of Natural History*, 6: 84–89.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit. Pars VII. Crustacea Anomura. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 10(7): 225–252 [Pages 263-290 on separate].

Stimpson, W. 1859. Notes on North American Crustacea in the Museum of the Smithsonian Institution No. 1. *Annals of the Lyceum of Natural History, New York*, 7(1962): 49–93.

Stimpson, W. 1860. A trip to Beaufort, N. Carolina. *American Journal of Science and Arts, Series 2*, 29(2): 442–445.

Stimpson, W. 1862. Notes on North American Crustacea, No. II. *Annals of The Lyceum of Natural History of New York*, 7(1): 176–246.

Stimpson, W. 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida by L.F. de Pourtales, Assist. U. S. Coast Survey. Part I. Brachyura. *Bulletin of the Museum of Comparative Zoölogy at Harvard College,*, 2(1–5): 109–160.

Stimpson, W. 1873. On some California Crustacea. *Proceedings of the California Academy of Natural Science (2nd ed.)*, 1(1854–1857): 1–88.

Stoliczka, F. 1871. Observations on fossil crabs from Tertiary deposits in Sind and Kutch. *Memoirs of the Geological Survey of India, Palaeontologica Indica, (7) (14)*, 1(1): 1–16.

Suthers, I. M., and Anderson, D. T. 1981. Functional morphology of mouthparts and gastric mill of *Ibacus peronii* (Leach) (Palinura: Scyllaridae). *Australian Journal of Marine and Freshwater Research*, 32: 931–944.

Swofford, D. L. 1999. PAUP*: Phylogenetic Analysis Using Parsimony, Version 4b. Illinois Natural History Survey, Champaign, Illinois.

Tan, S. H., and Ng, P. K. L. 2007. Descriptions of new genera from the subfamily Parthenopinae (Crustacea: Decapoda: Brachyura: Parthenopidae). *The Raffles Bulletin of Zoology*, Supplement No. 16: 95–119.

Tanaka, G., Smith, R. J., Siveter, D. J., and Parker, A. R. 2009. Three-dimensionally preserved decapod larval compound eyes from the Cretaceous Santana Formation of Brazil. *Zoological Science*, 26(12): 846–850.

Tanase, H. 1967. Preliminary notes on zoea and megalopa of the giant spider crab, *Macrocheira kaempferi* de Haan. *Publications of the Seto Marine Biological Laboratory*, 15(4): 303–309.

Tavares, M. 2003. A new theoretical approach for the study of monophyly of the Brachyura (Crustacea: Decapoda) and its impact on the Anomura. *Memoirs of Museum Victoria*, 60(1): 145-149.

Távora, V., Mesquita, N., de Souza, S. R., Cacela, A. S. M., and Teixeira, S. G. 2002. Sistemática e tafonomia dos crustáceos decápodes da ecofácies Capanema da Formação Pirabas (Mioceno Inferior), Estado do Pará. *Brazilian Journal of Geology*, 32(2): 223–230.

Távora, V., de Miranda, V. F. O., Viegas, L. G. F., and Galvão, P. H. F. 2005. Novos registros de crustáceos decápodes do Cenozóico (Paleoceno e Mioceno Inferior) do Brasil. *Brazilian Journal of Geology*, 35(3): 393–400.

Távora, V., and Dias, J. J. 2016. New records of decapods in Pirabas Formation (Miocene), Pará State, Brazil. *Annals of Aquaculture and Research*, 3(2): 1019.

Távora, V., Dias, J. J., Silva, M. C., Santos Sobral, A. d. C., and da Silva Franca, A. M. 2016. Crustáceos Ranినídeos da Formação Maria Farinha (Paleoceno-Eoceno), Estado de Pernambuco, Brasil. *Anuário do Instituto de Geociências - UFRJ*, 39(3): 32–40.

Tessier, G., Beschin, C., Busulini, A., and De Angeli, A. 1999. Nuovi Brachiuri Eocenici nella cava “Main” di Arzignano (Vicenza - Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali*, 24: 93–105.

Tetlie, O. E., and Poschmann, M. 2008. Phylogeny and palaeoecology of the Adelophthalmoidea (Arthropoda; Chelicerata; Eurypterida). *Journal of Systematic Palaeontology*, 6(02): 237-249.

Todd, J. A., and Collins, J. S. H. 2005. Neogene and Quaternary crabs (Crustacea, Decapoda) collected from Costa Rica and Panama by members of the Panama Paleontology Project. *Bulletin of the Mizunami Fossil Museum*, 32: 53–85.

Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A., and Minh, B. Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*.

Tsang, L. M., Ma, K. Y., Ahyong, S. T., Chan, T.-Y., and Chu, K. H. 2008. Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Molecular Phylogenetics and Evolution*, 48(1): 359–368.

Tsang, L. M., Chan, T.-Y., Ahyong, S. T., and Chu, K. H. 2011. Hermit to king, or hermit to all: Multiple transitions to crab-like forms from hermit crab ancestors. *Systematic Biology*, 60(5): 616–629.

Tsang, L. M., Schubart, C. D., Ahyong, S. T., Lai, J. C. Y., Au, E. Y. C., Chan, T.-Y., Ng, P. K. L., and Chu, K. H. 2014. Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution*, 31(5): 1173–1187.

Tucker, A. B., and Feldmann, R. M. 1990. Fossil decapod crustaceans from the lower Tertiary of the Prince William Sound region, Gulf of Alaska. *Journal of Paleontology*, 64: 409–427.

Tucker, A. B. 1995. A systematic evaluation of fossil Raninidae from the Twin River Group, Olympic Peninsula, Washington, and a re-examination of the Raninidae. (p. 363). Kent, Ohio: Kent State University.

Tucker, A. B. 1998. Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species. *Proceedings of the Biological Society of Washington*, 111(2): 320–371.

Türkay, M. 1970. Die Gecarcinidae Amerikas mit einem Anhang über *Ucides* Rathbun. *Senckenbergiana Biologica*, 51(5/6): 333–354.

van Bakel, B. W. M., Guinot, D., Artal, P., Fraaije, R. H. B., and Jagt, J. W. M. 2012a. A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa*, 3215: 1–216.

van Bakel, B. W. M., Guinot, D., Jagt, J. W. M., and Fraaije, R. H. B. 2012b. *Mithracites takedai*, a new homoloid crab (Decapoda, Brachyura) from the Lower Cretaceous (Aptian) of Colombia. In Komatsu, H., Okuno, J. and Fukuoka, K. (Eds) *Studies on Eumalacostraca: a homage to Masatsune Takeda. Crustaceana Monographs.* 17, 81–90 pp.

van Bakel, B. W. M. 2013. Preservation of internal pleurites in a new palaeocorystid crab (Crustacea, Brachyura, Raninoidia) from the Cenomanian (Upper Cretaceous) of Poitou-Charentes, France. *Zootaxa*, 3701(3): 322–328.

Van Straelen, V. 1925. Contribution à l'étude des crustacés décapodes de la période Jurassique. *Mémoires de l'Académie Royale de Belgique, Classe des Sciences, series 2*, 7: 1–462.

Van Straelen, V. 1933a. Sur des crustacés décapodes cénozoïques du Venezuela. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 9(10): 1–11.

Van Straelen, V. 1933b. Sur des crustacés décapodes de l'Eocène supérieur de l'Ile Bonaire. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 9(23): 1–4.

Van Straelen, V. 1936. Crustacés décapodes nouveaux ou peu connus de l'époque Crétacique. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 12(45): 1-49.

van Waveren, I. M., van Konijnenburg-van Cittert, J., Van der Burgh, J., and Dilcher, D. 2002. Macrofloral remains from the Lower Cretaceous of the Leiva region (Colombia). *Scripta Geologica*, 123: 1–39.

Vannier, J., Schoenemann, B., Gillot, T., Charbonnier, S., and Clarkson, E. 2016. Exceptional preservation of eye structure in arthropod visual predators from the Middle Jurassic. *Nature Communications*, 7.

Varela, C., and Rojas-Consuegra, R. 2009. Crustáceos (Decapoda: Brachyura) fósiles de Cuba. *Solenodon*, 8: 118–123.

Varela, C., and Rojas-Consuegra, R. 2011a. El registro fósil de los crustáceos decápodos (Arthropoda, Crustacea) marinos de Cuba. *IX Congreso Cubano de Geología (Memorias)*: 1–10.

Varela, C., and Rojas-Consuegra, R. 2011b. Especie nueva de *Eriosachila* Blow and Manning, 1996, (Crustacea: Decapoda), de la Formación Colón, Cuba. *Novitates Caribaea*, 4: 17–20.

Varela, C., and Rojas-Consuegra, R. 2011c. Crustáceos fósiles (Decapoda: Brachyura) de la Formación Colón, Matanzas, Cuba. *Solenodon*, 9: 66–70.

Varela, C., and Schweitzer, C. E. 2011. A new genus and new species of Portunidae Rafinesque, 1815 (Decapoda, Brachyura) from the Colón Formation, Cuba. *Bulletin of the Mizunami Fossil Museum*, 37: 13-–16.

Varela, C. 2013. Nuevos datos sobre los crustáceos fósiles (Decapoda: Brachyura) de Cuba. *Solenodon*, 11: 1–5.

Vega, F. J., and Perrillat, M. C. 1989. Una especie nueva de cancrejo del género *Costacopluma* (Crustacea: Decapoda: Retroplumidae) del Maastrichtiano de Nuevo León, México. *Universidad Nacional Autónoma, Instituto de Geología, Revista*, 8: 84–87.

Vega, F. J., and Feldmann, R. M. 1991. Fossil crabs (Crustacea: Decapoda) from the Maastrichtian Difunta Group, northeastern Mexico. *Annals of Carnegie Museum*, 60(2): 163–177.

Vega, F. J., and Feldmann, R. M. 1992. Occurrence of *Costacopluma* (Decapoda: Brachyura: Retroplumidae) in the Maastrichtian of southern Mexico and its paleobiogeographic implications. *Annals of Carnegie Museum*, 61(2): 133–152.

Vega, F. J., Feldmann, R. M., and Sour-Tovar, F. 1995a. Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cárdenas Formation, East-Central Mexico. *Journal of Paleontology*, 69(2): 340–350.

Vega, F. J., Feldmann, R. M., and Villalobos-Hiriart, J. L. 1995b. Additions to the crustacean (Decapoda) fauna from the Portrerillos Formation (Late Cretaceous) in northeastern Mexico. *Annals of Carnegie Museum*, 64(3): 39–49.

Vega, F. J., Feldmann, R. M., Ocampo, A. C., and Pope, K. O. 1997. A new species of late Cretaceous crab (Brachyura: Carcineretidae) from Albion Island, Belize. *Journal of Paleontology*, 71(4): 615–620.

Vega, F. J., Feldmann, R. M., Villalobos-Hiriart, J. L., and Gio-Argíez, R. 1999. A new decapod Fauna from the Miocene Tuxpan Formation, Eastern Mexico. *Journal of Paleontology*, 73(3): 407–413.

Vega, F. J., Cosma, T., Coutiño, M. A., Feldmann, R. M., Nyborg, T., Schweitzer, C. E., and Waugh, D. A. 2001a. New Middle Eocene decapods (Crustacea) from Chiapas, Mexico. *Journal of Paleontology*, 75: 929–946.

Vega, F. J., Feldmann, R. M., García-Barrera, P., Filkorn, H., Pimentel, F., and Avendaño, J. 2001b. Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuautla Formation in Chiapas, southeast Mexico. *Journal of Paleontology*, 75(2): 319–329.

Vega, F. J., Bruce, N. L., Serrano, L., Bishop, G. A., and Perrilliat, M. d. C. 2005. A review of the Lower Cretaceous (Tlayúa Formation: Albian) Crustacea from Tepexi de Rodríguez, Puebla, Central Mexico. *Bulletin of the Mizunami Fossil Museum*, 32: 25–30.

Vega, F. J., García-Barrera, P., Perrillat, M. C., Coutiño, M. A., and Mariño-Pérez, R. 2006a. El Espinal, a new plattenkalk facies locality from the Lower Cretaceous Sierra Madre Formation, Chiapas, southeast Mexico. *Revista Mexicana de Ciencias Geológicas*, 23(3): 323–333.

Vega, F. J., Nyborg, T. G., and Perrilliat, M. D. C. 2006b. Mesozoic and Tertiary Decapod Crustacea from Mexico. In Vega, F. J., Nyborg, T. G., Perrilliat, M. D. C., Montellano-Ballesteros, M., Cevallos-Ferriz, S. R. S. and Quiroz-Barroso, S. A. (Eds) *Studies on Mexican Paleontology*, 79-100 pp. Dordrecht. Springer Netherlands.

Vega, F. J., Nyborg, T., Fraaye, R. H., and Espinosa, B. 2007a. Paleocene decapod Crustacea from the Rancho Nuevo Formation (Parras Basin-Difunta Group), Northeastern México. *Journal of Paleontology*, 81(6): 1432–1441.

Vega, F. J., Nyborg, T., Rojas-Briceño, A., Patarroyo, P. C., Luque, J., Porras-Múzquiz, H., and Stinnesbeck, W. 2007b. Upper Cretaceous Crustacea from Mexico and Colombia: Similar faunas and environments during Turonian times. *Revista Mexicana de Ciencias Geológicas*, 24: 403–422.

Vega, F. J., Nyborg, T., Coutiño, M. A., and Hernández-Monzón, O. 2008. Review and additions to the Eocene decapod Crustacea from Chiapas, Mexico. *Bulletin of the Mizunami Fossil Museum*, 34: 51–71.

Vega, F. J., Nyborg, T., Coutiño, M. A., Solé, J., and Hernández-Monzón, O. 2009. Neogene Crustacea from Southeastern Mexico. *Bulletin of the Mizunami Fossil Museum*, 35: 51–69.

Vega, F. J., Nyborg, T., Kovalchuk, G., Luque, J., Rojas-Briceño, A., Patarroyo, P. C., Porras-Múzquiz, H., Armstrong, A., Bermúdez, H., and Garibay, L. 2010. On some Panamerican Cretaceous crabs (Decapoda: Raninoida). *Boletín de la Sociedas Geológica Mexicana*, 62(2): 263–279.

Vega, F. J., Phillips, G. E., Nyborg, T., Flores-Ventura, J., Clements, D., Espinosa, B., and Solís-Pichardo, G. 2013. Morphology and size variation of a portunoid crab from the Maastrichtian of the Americas. *Journal of South American Earth Sciences*, 47(0): 116–135.

Vega, F. J., Jackson, J., and Ossó, À. 2014. Exceptional preservation of a late Cenomanian (Late Cretaceous) crab from Texas, U.S.A. *Boletín de la Sociedad Geológica Mexicana*, 66(1): 215–221.

Vega, F. J., Centeno-García, E., Martínez-Díaz, J. L., Espinosa, B., and Ventura, J. F. 2016. Late Cretaceous Brachyuran Crustaceans from Northeastern Mexico. In Khosla, A. and Lucas, S. G. (Eds) *Cretaceous Period: Biotic Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin.* 71, 307–315 pp.

Vehof, J., Scholtz, G., and Becker, C. 2018. *Paradorippe granulata* – A crab with external fertilization and a novel type of sperm storage organ challenges prevalent ideas on the evolution of reproduction in Eubrachyura (Crustacea: Brachyura: Dorippidae). *Arthropod Structure & Development*, 47: 82–90.

Vermeij, G. J. 1973. Adaptation, versatility, and evolution. *Systematic Biology*, 22(4): 466–477.

Vermeij, G. J. 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology*, 3: 245–258.

Vermeij, G. J., and Portell, R. W. 2013. New fossil records of Neritidae (Gastropoda) from Florida, U.S.A. *Cainozoic Research*, 10(1–2): 53–57.

Vermeij, G. J. 2015. Forbidden phenotypes and the limits of evolution. *Interface Focus*, 5(6): 20150028.

Vernygora, O., Murray, A. M., Luque, J., Ruge, M. L. P., and Fonseca, M. E. P. 2017. A new Cretaceous dercetid fish (Neoteleostei: Aulopiformes) from the Turonian of Colombia. *Journal of Systematic Palaeontology*: 1-15.

Vía Boada, L. 1959. Decápodos fósiles del Eoceno español. *Boletín del Instituto Geológico y Minero de España*, 70: 331–402.

Vía Boada, L. 1966. Pinnixa (Palaeopinnixa) mytilicola, nuevo braquiuro fósil, en el mioceno marino del Vallés (Barcelona). *Acta geológica hispánica*, 1(4): 1–4.

Villamil, T. 1998. Chronology, relative sea-level history and new sequence stratigraphic model for basinal Cretaceous facies of Colombia. In Pindell, J. and Drake, C. (Eds) *Eustasy and Tectonostratigraphic Evolution of Northern South America.* 58, 161–216 pp. SEPM Special Publication.

Villamil, T., and Arango, C. 1998. Integrated stratigraphy of latest Cenomanian-early Turonian facies of Colombia. In Pindell, J. and Drake, C. (Eds) *Eustasy and Tectonostratigraphic Evolution of Northern South America. SEPM Special Publication.* 58, 129–159 pp.

Vogt, K. 1975. Zur Optik des Flußkrebsauges. *Z Naturforsch*, 32.

Vogt, K. 1980. Die Spiegeloptik des Flußkrebsauges. *Journal of Comparative Physiology A*, 135: 1–19.

Voise, J., and Casas, J. 2009. The management of fluid and wave resistances by whirligig beetles. *Journal of The Royal Society Interface*, 7(43): 343–352.

Ward, M. 1942. A new genus and eight new species of Brachyura from Mauritius and the Chagos Archipelago. *Mauritius Institute Museum*, 2: 39–48, pls. 32–34.

Weber, F. 1795. Nomenclator entomologicus secundum entomologiam systematicam... Fabricii, adjectis speciebus recens detectis et varietatibus: Chilonii and Hamburgi.

White, A. 1846. Notes on four new genera of Crustacea. *The Annals and Magazine of Natural History [series 1]*, 18: 176–178.

White, A. 1847. List of the specimens in the collection of the British Museum. London: British Museum.

White, A. 1848. Short descriptions of new of little-known decapod Crustacea, 2. In: November 23, 1847. William Yarrell, Esq. Vice President, in the chair. *Proceedings of the Zoological Society of London*, (15)179 ((1847)): 222–228.

Williams, A. B. 1974. The swimming crabs of the genus *Callinectes*. *Fishery Bulletin*, 72(3): 685–798.

Williams, A. B. 1976. Distinction between a Gulf of Mexico and a Carolinian Atlantic species of the swimming crab *Ovalipes* (Decapoda: Portunidae). *Proceedings of the Biological Society of Washington*, 89(14): 205–214.

Williams, A. B., and Rona, P. A. 1986. Two new caridean shrimps (Cresillidae) from a hydrothermal field on the Mid-Atlantic Ridge. *Journal of Crustacean Biology*, 6: 446–462.

Williams, M. J. 1978. Opening of bivalve shells by the mud crab *Scylla serrata* Forskål. *Australian Journal of Marine and Freshwater Research, 29: 699-702.*, 29: 699–702.

Windsor, A. M., and Felder, D. L. 2014. Molecular phylogenetics and taxonomic reanalysis of the family Mithracidae MacLeay (Decapoda : Brachyura : Majoidea). *Invertebrate Systematics*, 28: 145–173.

Withers, T. H. 1922. On a new brachyurous crustacean from the Upper Cretaceous of Jamaica. *Annals and Magazine of Natural History*, 9(10): 534–541.

Withers, T. H. 1924a. Decapod crustaceans from the Oligocene of Anguilla. *Annals and Magazine of Natural History (series 9)*, 14: 225–233.

Withers, T. H. 1924b. Some Cretaceous and Tertiary Decapod Crustaceans from Jamaica. *Journal of Natural History Series 9*, 9(13): 81–93.

Withers, T. H. 1927. *Ranina trechmanni*, a new Cretaceous crab from Jamaica. *Geological Magazine*, 64: 176–180.

Wolfe, J. M. 2017. Metamorphosis is ancestral for crown euarthropods, and evolved in the Cambrian or earlier. *Integrative and Comparative Biology*.

Woods, H. 1922. Crustacea from the Eocene deposits of Peru. In Bosworth, T. O. (Ed) *Geology of the Tertiary and Quaternary Periods in the northwest part of Peru*, 114–118 pp. London. Macmillan and Co.

Woodward, H. 1866. Note on a new species of *Ranina* (*Ranina porifera*) from the Tertiary strata of Trinidad. *Quarterly Journal of the Geological Society of London*, 22: 591–592.

Wright, A. M., and Hillis, D. M. 2014. Bayesian analysis using a simple likelihood model outperforms parsimony for estimation of phylogeny from discrete morphological data. *PLoS ONE*, 9(10): e109210.

Wright, C. W., and Collins, J. S. H. 1972. British Cretaceous crabs. *Palaeontographical Society Monographs*, 126(533): 1–113.

Xu, Z., Lenaghan, S. C., Reese, B. E., Jia, X., and Zhang, M. 2012. Experimental studies and dynamics modeling analysis of the swimming and diving of whirligig beetles (Coleoptera: Gyrinidae). *PLoS Computational Biolology*, 8(11): e1002792.

Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular Evolution*, 39(3): 306-314.

Appendix 1

This supplemental table accompanies Chapter 3. A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: frog first or crab first?

Supplemental Table S3.1. Character dataset for 74 adult morphological characters scored for *Araripecarcinus* Martins–Neto, 1987, included in Analysis I (Fig. 3.4) following the character list and scorings of Karasawa *et al.* (2011, pp. 526–529, table 2). Dagger † denotes that *Araripecarcinus* is only known as fossil. Character scores: undetermined or not preserved (?), inapplicable characters states (-).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
†***Araripecarcinus***	1	1	0	1	1	0	?	?	?	?	?	?	?	1	?	0	?	?	?	0

	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
†***Araripecarcinus***	?	?	?	1	0	1	0	?	?	1	1	1	?	0	?	1	1	?	0	?

	41	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
†***Araripecarcinus***	?	?	?	?	?	?	?	1	?	?	1	0	?	?	?	?	?	?	?	?

	61	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**
†***Araripecarcinus***	?	?	1	?	?	1	1	?	1	0	?	?	?	?

Supplemental Table S3.2. Character list for 44 adult morphological characters scored for 14 taxa included in Analysis II (Fig. 3.5A; Supplementary Table S3.3). Character scores: undetermined or not preserved (?), inapplicable characters states (-). Base character list modified after Karasawa *et al.* (2011) and van Bakel *et al.* (2012a).

1. Carapace proportions elongate (0) as long as wide or wider (1)
2. Anterolateral margins indistinct (0) distinct (1)
3. Spines or teeth on anterolateral margins absent (0) present (1)
4. Spines on posterolateral margin absent (0) present (1)
5. Carapace with well differentiated anterolateral and posterolateral margins absent (0) present (1)
6. Posterolateral margins rounded not defined (0) defined (1)
7. Posterior margin concave (0) straight to convex (1)
8. Orbit not defined (0) defined (1)
9. Inner orbital angle not defined (0) defined (1)
10. Upper orbital fissures absent (0) present (1)
11. Subhepatic swelling present (0) absent (1)
12. Antennal groove present (0) absent (1)
13. Cervical groove distinct (0) indistinct (1)
14. Postcervical groove present (0) absent (1)
15. Branchiocardiac groove distinct (0) indistinct (1)
16. Axial longitudinal ridge or tubercles absent (0) present (1)
17. Branchial longitudinal ridges or tubercles absent (0) present (1)
18. Cervical or branchiocardiac groove reaching ventral carapace (0) ending at anterolateral margin or before reaching it (1)
19. Intestinal region very narrow and limited by branchiocardiac grooves (0) wide (1)
20. Buccal cavern wide (0) elongated triangular (1)
21. Thoracic sternum narrow (0) wide (1)
22. Posterior sternites wide (0) narrow and reduced (1)
23. Sterno pleonal cavity absent (0) present (1)
24. Sella turcica absent (0) present (1)
25. Spermatheca if present paired (0) united (1)
26. Pleon not folding (0) folding (1)
27. Pleonal pleura well developed (0) reduced (1)
28. Articulating rings of pleon present (0) absent (1)
29. Pleonal locking absent (0) present (1)
30. Maxilliped 3 pediform (0) operculiform (1)
31. Maxilliped 3 with two plains absent (0) present (1)
32. Maxilliped 3 with crista dentata present (0) absent (1)
33. Maxilliped 3 coxa large touching each other (0) small not touching each other (1)
34. Palp of maxilliped 3 merus distal position (0) inner mesial position (1)
35. Palp of maxilliped 3 merus different plane (0) same level to merus (1)
36. Pereiopods 2 to 4 form normal (0) wide flattened (1)
37. Pereiopod 5 wide flattened absent (0) present (1)
38. Pereiopods 4 to 5 condition normal (0) P5 dorsal (1) P4 and P5 dorsal (2)
39. Pereiopods 4 to 5 size normal (0) P5 reduced (1) P4 to P5 reduced (2)
40. Anterolateral corners of sternite 4 in contact with pterygostome absent (0) present (1)
41. Milne-Edwards openings absent (0) present (1)
42. Thoracic sternum pleurites no exposed (0) partially exposed (1)
43. Sterno-pleural extensions absent (0) present (1)
44. Female sexual openings coxal (0) sternal (1)

Supplemental Table S3.3. Character dataset for 44 adult morphological characters scored for 14 taxa included in the phylogenetic analysis (Fig. 5A; Table 2). Taxa indicated by † only known as fossil. Character scores: undetermined or not preserved (?), inapplicable characters states (-), polymorphism (0&1). Base character list modified after Karasawa et al. (2011) and Van Bakel et al. (2012a).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Astacidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
†Eocarcinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Homolodromiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyreididae	0	1	0&1	0	0	1	1	1	1	1	1	1	1	1	0&1	0	0	1	1	1
Raninidae	0	1	0&1	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
Symethidae	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
†Camarocarcinidae	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0&1	0	0&1	1	1
†Cenomanocarcinidae	1	1	1	1	1	1	0&1	1	1	1	1	1	0&1	1	0&1	1	1	1	1	1
†Necrocarcinidae	1	1	1	1	1	1	0&1	1	1	1	1	1	0	1	0&1	0&1	0&1	0&1	1	1
†Orithopsidae	1	1	1	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	1
†Palaeocorystidae	0	1	1	0	1	1	0	1	1	1	1	1	0&1	1	0&1	0&1	0	0&1	1	1
†*Araripecarcinus*	1	1	0	0	1	1	?	?	?	?	?	?	0	?	?	?	?	0	?	1
Portunidae	1	1	1	0	1	1	1	1	1	1	1	1	0&1	1	1	0	0	1	1	0
Carcinidae	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	-	1	0

	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Astacidea	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
†Eocarcinidae	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?	0	0	0	0	?
Homolodromiidae	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	2	2	0
Lyreididae	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0&1
Raninidae	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0&1	1
Symethidae	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1
†Camarocarcinidae	0	0	0	?	?	1	?	?	1	1	1	1	1	?	?	?	0	?	?	0
†Cenomanocarcinidae	0	0	0	?	0	1	1	1	1	1	1	1	1	0	1	0&1	0	1	1	0
†Necrocarcinidae	0	0	0	?	?	1	1	1	?	1	1	1	1	?	?	0	0	1	1	0
†Orithopsidae	0	0	0	?	?	1	1	1	1	?	?	?	1	?	?	?	0	?	?	0
†Palaeocorystidae	0	0	0	?	0	1	1	1	0&1	1	1	1	1	0	1	1	0	1	1	0
†***Araripecarcinus***	0	0	0	?	?	?	?	1	?	?	?	?	1	?	?	1	0	1	1	0
Portunidae	1	0	1	1	-	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0
Carcinidae	1	0	1	1	-	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0

	41	**42**	**43**	**44**
Astacidea	?	0	0	0
†Eocarcinidae	?	?	?	?
Homolodromiidae	1	0	0	0
Lyreididae	0&1	1	1	0
Raninidae	0	1	1	0
Symethidae	0	1	1	0
†Camarocarcinidae	1	0	0	0
†Cenomanocarcinidae	1	0	0	0
†Necrocarcinidae	1	0	0	0
†Orithopsidae	1	0	0	0
†Palaeocorystidae	?	0	0	0
†***Araripecarcinus***	?	?	?	?
Portunidae	1	0	0	1
Carcinidae	1	0	0	1