Neohelice granulata, a Model Species for Studies on Crustaceans, Volume I

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Life History and Ecology

Edited by

Tomás A. Luppi and Enrique M. Rodriguez

Cambridge Scholars Publishing

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This book first published 2020

Cambridge Scholars Publishing

Lady Stephenson Library, Newcastle upon Tyne, NE6 2PA, UK

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

ISBN (10): 1-5275-5003-6
ISBN (13): 978-1-5275-5003-2

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ANATOMY AND PHYSIOLOGY

FOREWORD

Neohelice granulata – a model species for studies on crustaceans.

Long species monographs seem to be a thing of the past, probably because few researchers have the luxury or dedication to be able to focus long-term research efforts exclusively on one species or a group of species. This up-to-date monograph on *Neohelice granulata* proves the great value that such monographs still have in current times. While in the past, species or taxon-focused monographs were typically written by single researchers who had spent their entire career investigating their favourite organisms, this monograph on *N. granulata* is a group effort gathering a total of 77 authors, primarily from Argentina. This is a gigantic achievement for the editors, who were able to shepherd such a diverse group of authors for this monograph with a total of 33 chapters. This monograph is published in two volumes, but it is a unit work, indivisible in its conception, realization and integration, evidenced by its numerous cross-references between chapters and volumes.

The result of this effort provides an overview about one of the best-studied crustacean species of the past few decades. From reading some of the chapters, it becomes evident that this is not only a collection of chapters about *N. granulata*, but these volumes are also testimony to the long-term research commitment of the Argentinian crustacean community. Collectively, they have worked over decades to investigate all aspects of the biology and life history of this intertidal crab. These volumes demonstrate the community effort put into every single chapter and becoming evident on almost any single page. At least two authors write most of the chapters, and many by more than two authors, furthermore underscoring this collaborative effort. The editors and their fellow authors are to be congratulated for pulling off this group achievement!

Each volume is divided into two sections, each with a brief introductory preface by one of the eminent scholars in the field. In the first section on life history and developmental biology, the eight chapters explore the early life of *N. granulata*, from embryonic development to larval life. The authors focus on the pelagic stages, settlement biology, and life cycles. In the section on ecology and ecosystem role of the crab, the eight chapters examine *N. granulata*'s predators, forms of food acquisition and the complexity of its mating system as well as their effects on habitat structure and species interactions. The eight chapters in the section on neurobiology cover topics ranging from sensory systems to neural

integration including memory and learning. Finally, in the section on anatomy and physiology, the authors present information on the reproductive system, investment in growth and reproduction, general metabolic strategies and respiration of this fascinating crab living at the interface between air and water.

The individual chapters are all relatively concise, and they are richly illustrated, making the reading a pleasant experience. All chapters are written in clear language, making them accessible to readers from related disciplines or people interested in the general biology and ecology of crustaceans.

This work presents *N. granulata* as an ideal model species for future studies on climate change, pollution, habitat degradation, or species invasion. The distributional range of *N. granulata* is one of the areas in the world's oceans that have and will continue to experience substantial changes in seawater temperatures. Not surprisingly, *N. granulata* is increasingly confronted with invasive species, which either have been expanding their geographic ranges or which have been introduced by human activities, e.g. ship transport. For example, in large parts of its natural habitat *N. granulata* will soon be confronted with one of the most aggressive invaders around the world, the shore crab *Carcinus maenas*, which has already established a foothold in Argentinian Patagonia, and is steadily expanding its invaded range to the north. Additionally, *N. granulata* is exposed to industrial and coastal activities, and one of the chapters in the volume on endocrine disruption examines the effects of pollution on reproductive traits and success in *N. granulata*. This is the only chapter on anthropogenic impacts on this marvellous little crab from the South-West Atlantic, but future studies on human impacts will be able to build on the enormous and complete knowledge provided in this volume.

These volumes should be an inspiration for others, who might have similarly rich and integral information on their local crab species – I could easily envision several well-studied crabs that would merit a similar volume.

In the meantime, the scene is set for *Neohelice granulata* to serve as a model organism for scientists from different fields and regions of the world. This work provides researchers with all the basic knowledge needed to thoroughly examine whether and how this common intertidal crab is adapting to the changes occurring in their natural habitats.

Martin Thiel, Coquimbo, Chile

PREFACE

The idea of editing this book arose from the need to compile as much information as possible about the biology of a species that has been a model for many years for several research groups, mainly from Argentina and Brazil. Ernesto Sábato, an Argentine physicist and writer, used to say that the scientific world is evolving more and more towards specialization, being increasingly difficult or rare to find "generalists" who summarize and obtain conclusions from a large amount of specific information accumulated on each particular topic. This book does not pretend to obtain such conclusions, but to facilitate the reader to integrate the entire results obtained by most of the groups that have worked with this model species.

This book was in some way inspired by several forerunning events, at first, the workshops on "Cangrejos and Cangrejales", held in various venues. The first one took place in Buenos Aires, in June 1988, where research groups from Argentina, Brazil, and Uruguay participated; most of these groups were just beginning with their research in *Neohelice granulata*, a species characterized by the pioneer Enrique Boschi as the most conspicuous of the so-called "Cangrejal Bonaerense". The second workshop was held in Mar del Plata in November 1994 and was able to confirm the important progress of the many participant groups. In December 1996 was held the third workshop in Rio Grande, Brazil, and the fourth and last was held in Buenos Aires, in April 1999. All these meetings bolstered a fruitful exchange of information and discussion of results, also favouring the development of several joint projects between different research groups. However, the closest historical background of this book dates from the meeting that took place in Rio Grande, Brazil in April 2005, where it was proposed the publication of a book about the biology of *Neohelice*, which unfortunately did not materialize. Today we can say with pride that finally this task has been fulfilled.

This book not only intends to be a collection of information about *N. granulata* and a data source for this species, but it also aims to be a reference book for any researcher studying the biology of crustaceans, and even a reference for other disciplines in which the species serves as a representative model. The reader will save a lot of time in the search and integration of information, considering that the book concentrates in a single source practically all existing references focusing on this crab. Any researcher, who initiates a project concerned either about the environment inhabited by the crab or any other subject in which the crab is a model

system, should necessarily refer to this book as a source of information. Finally, the third objective of this book is to contribute to academic teaching, both undergraduate and post-graduate, as a book for study and consultation, potentially useful in many areas of biology, anatomy, physiology, and invertebrate ecology.

Indeed, *N. granulata* is nowadays one of the most studied crab species. This species has been a very successful model for studies on ecophysiology: embryonic, larval, juvenile, and adult development; neurobiology; phenotypic plasticity; and an excellent model for understanding the ecosystem function of marine and estuarine species. On the other hand, the large body of literature produced during the last decades has been intimately linked to the training of graduate students and post-graduate researchers in Brazil, Uruguay, Argentina, and Germany, contributing to the development of cooperation projects among researchers from most of the countries above mentioned.

This book is divided into two volumes. The first volume comprises 17 chapters grouped into two main sections: "Life history traits and development" and "Inter-specific relationships, behavioural ecology and ecosystem functionality". On the other hand, the second volume comprises 16 chapters, also grouped into two sections: "Neurobiology" and "Anatomy and physiology". Both volumes bring together more than 70 authors from 6 countries. Each of the main sections is prefaced by a specialist, "Life history traits and development" by Dr. Klaus Anger, "Inter-specific relationships, behavioural ecology and ecosystem functionality" by Dr. Oscar Iribarne, "Neurobiology" by Drs. Daniel Tomsic and Arturo Romano, and "Anatomy and physiology" by Dr. Enrique Rodriguez. Each of them gives his vision about the relevance that *N. granulata* in the development of each research area. In an appendix, we include the updated list of all published papers, as an additional contribution to the edition of the different chapters.

We do not want to end this prologue without first thanking each of the colleagues who have devoted their time to the development of one or more chapters, and who have responded promptly to our demands for editing. Our thanks also to the reviewers of each chapter, as well as to those who have prefaced each section of the book. At the same time, we want to invite colleagues who work in *Neohelice*, but for some reason have not been able to contribute to this first edition, to contact us and contribute to future editions of the book.

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NEOHELICE GRANULATA BACKGROUND KNOWLEDGE

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The burrowing and semi-terrestrial crab *Neohelice granulata* Dana, 1851, (formerly known as *Chasmagnathus granulatus*) is a key South American species, endemic to the warm temperate coast of the southwestern Atlantic. This species is found along more than 4000km of the coastline of Argentina, Uruguay, and Brazil. Its geographical distribution (Fig. 1) ranges from northern Patagonia (42°25′S; Riacho San José, Chubut Province, Argentina) to southern Brazil (22°57′S; Lagoa Araruama, Rio de Janeiro State, Brazil).

It is strictly associated with tidal flats in estuaries, bays, and coastal lagoons, where the halophyte cordgrasses are *Sporobolus densiflorus* (previously known as *Spartina densiflora*), *Sporobolus alterniflorus* (previously known as *Spartina alterniflora*) and *Sarcoconia perennis* form marshes located in the middle and upper intertidal zone. *Neohelice granulata* has a complex life cycle with benthic adult and juvenile stages, and a planktonic phase (four or five zoeae and one megalopa stage). Larval release from females is synchronous, and freshly hatched zoeae are exported from several parental habitats, e.g. those with low salinity waters on ebb tides. These larvae were only found in nearshore waters (marine or with moderately reduced salinities), which seem to be more favourable for development. The megalopa stage migrates from coastal waters to marine,

brackish and even limnetic habitats. It is capable of swimming actively and consequently, selectively settling near their respective adult populations, while moulting to the first juvenile stage.

The habitat of *N. granulata* includes different environmental conditions. Along with its extensive and yet discontinuous geographical distribution (» 22° latitude), they inhabit areas with highly variable tidal range, salinity, temperature, sediment, and biotic factors. As a consequence, crabs must face many challenges, for instance: from a few cms up to 9m of semidiurnal tide amplitudes, with a high variance in predictability; from near 0 up to 60psu of water salinity; from soft to hard substrata (muddy and cobble beaches, respectively), from high to low-quality food, and also facing different predation pressures. Besides, these crabs live in mudflats or salt marshes placed at different intertidal levels, where adults of both sexes and juveniles are intermixed, with various emersion-submersion patterns, burrow size, shape and dynamics, physical and chemical characteristics of water, feeding habits and activity level.

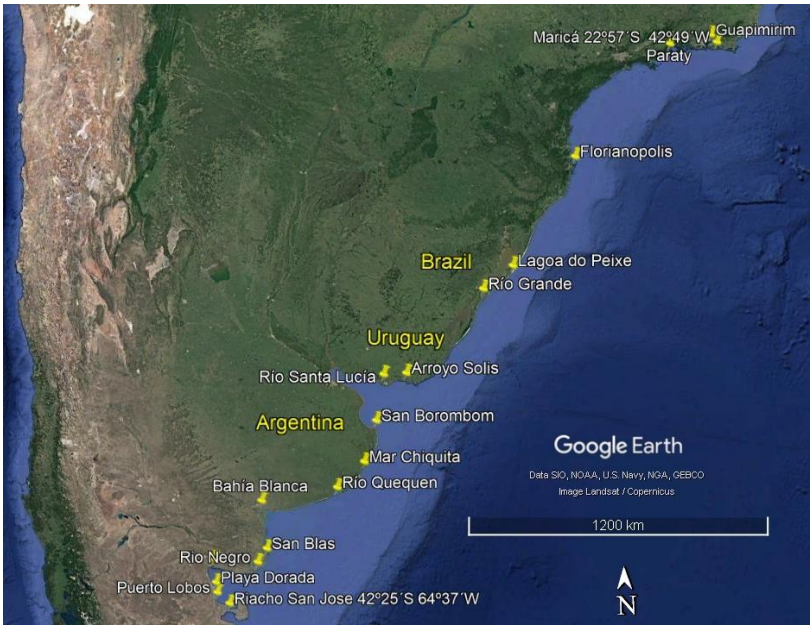

Figure 1. Locations where populations of *Neohelice granulata* have been recorded. The coordinates of the populations at the ends of the distribution are indicated.

High levels of genetic structure were detected among populations of *N. granulata* inhabiting the complete geographic range of the species, indicating that connectivity between adjacent sites may be limited to scales of hundreds of kilometres. However, such genetic disparity not always correlates with morphometric analysis; in fact, no clear geographical pattern of morphological differentiation could be observed.

Neohelice granulata digs semi-permanent burrows and is active both in air and water, given its bimodal respiration capacity. During low tides, crabs leave burrows and perform short "exploratory excursions", but they hide in the presence of aerial predators or cannibal behaviour. Crabs are also active underwater, carrying out longer excursions, especially during high tides, and their feeding activities rise dramatically in the vegetated habitat during flooding.

Juveniles and adults feed on saltmarsh plants and sediments. The proportion of each food item in the diet will depend on location, both on an intra-populational spatial scale (mudflat vs saltmarsh), and an inter-population scale; in both cases, marked differences can exist in the content of organic matter associated to sediments, therefore influencing several life-history traits such as growth, reproduction, and cannibalism.

Temperature and photoperiod are relevant environmental cues for reproduction. Ovaries develop under the control of several hormones, and marked differences among populations were noticed during the annual maturation cycles. Spawning is restricted to spring and summer in temperate sites, but ovigerous females can be found throughout the year in tropical populations. Number of eggs in each spawning, even higher than 30000, depends on crab size among other factors. The egg incubation period normally ranges from 15 to 20d, according to temperature and salinity. Fecundation is internal, and the mating system is flexible, with a combination of strategies depending on the size of crabs and type of burrows.

In temperate zones, sexual maturity is reached between one year and one year and a half, based on the time of the year when the first juvenile stage starts to grow. Longevity is estimated between two and a half and three and a half years, depending on environmental conditions and sex.

CHAPTER ONE

THE SOUTHWESTERN ATLANTIC INTERTIDAL CRAB *NEOHELICE GRANULATA* (DANA, 1852): HISTORY OF A SUCCESSFUL ANIMAL MODEL FOR SCIENTIFIC RESEARCH, FROM 19TH CENTURY NATURALISTS TO 21TH CENTURY LABORATORIES

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Discovery

The first scientific mention of *Neohelice granulata* was probably a manuscript note by Alcide d'Orbigny, a prominent French naturalist of the early and middle 18th Century who made major contributions in zoology, palaeontology, geology, archaeology and anthropology, and who named a large number of invertebrate species. D'Orbigny took part in a seven-year expedition (1826-1834) to South America as "*Naturaliste-voyageur du Muséum d'Histoire Naturelle*" of Paris and described his many findings in the book "*Voyage dans l'Amérique Méridionale*" (D'Orbigny 1835-1847). However, the text concerning the "*Ocypode à grosses pattes*" (*Ocypode* with gross legs) was found in the handwritten catalogue of his collections (Guinot and Cleva 2002):

«*Forme quadrangulaire, de très grosses pattes, gris bleu en dessus, rose violet en dessous. Habite depuis le 34° de latitude sud jusqu'au Rio Negro, 41° de latitude. Dans tous les lieux vaseux et tranquilles, tels*

qu'entrée des rivières, de ruisseaux salés, ou dans les herbes maritimes des côtes, dans les lieux où la mer bat peu. Ils se creusent des trous dans la vase mole, au niveau des hautes marées de vives eaux; c'est surtout le soir qu'ils sortent et qu'ils parcourent en tous sens la superficie de la vase; rarement ils entrent dans l'eau et ils abandonnent leur trous dès que l'eau le gagne. Ils sont très communs, surtout dans le fond de la Baie de St Blas.»

Guinot and Cleva (2002) included in their article an English translation and also a facsimile of this text. On its left border, there is a list of localities where *N. granulata* was found: Montevideo, "Plata", Bahía Blanca, Bahía San Blas and Rio Negro. These names remained unchanged, except the second (that probably corresponds to Bahía Samborombón as part of the Argentine coasts of the Río de la Plata), and their geographic coordinates are specified in Table 1.1.

D'Orbigny (1835-1847) described the coasts of one of those sites: Bahía Blanca Estuary. This is one of the largest intertidal mudflats in the Southwestern Atlantic and an extremely high proportion of its area is covered with burrows of *N. granulata* (Iribarne et al. 2004). Probably, Bahía Blanca Estuary holds the largest population of this species. D'Orbigny (1835-1847) wrote:

«*Tous les terrains des environs sont vaseux, et, sur les bords même, ne présentent qu'une vase plus molle et pleine de trous de crabes, ce qui leur a fait donner, par les habitans, le nom de cangrejales; car, à peine les chevaux y posent-ils les pieds de devant, qu'ils y tombent et s'y enfoncent jusquau ventre; quelquefois même il devient impossible de les en retirer, et ils y périssent.*»

Cangrejales (from the Spanish ''cangrejo'' = crab) was the name given by the inhabitants of this region to the large muddy tidal flats covered by *N. granulata* burrows, and this word is used until now. Nicely, a literary description of a ''cangrejal'', the crabs, and their burrows appeared in a famous novel that tells the adventures of a gaucho in the Argentine pampa (Don Segundo Sombra; Güiraldes 1926); this description agreed very much with D'Orbigny notes (1835–1947), in particular when it tells the story of horses that sunk in the mud and got stuck up to their bellies (see Spivak 2016).

Table 1.1. Geographic coordinates corresponding to D'Orbigny's findings of *Neohelice granulata.*

Site	Latitude; longitude
Montevideo (Uruguay)	34º54'S; 56º15'W
Samborombón Bay (Argentina)	from 35°26'S; 57°08'W to 36º18'S; 56º47'W
Bahía Blanca Estuary (Argentina)	from 39º26'S; 62°03'W to 39º00'S; 61º33'W
San Blas Bay (Argentina)	40°33'S; 62°14'W
mouth of Río Negro (Argentina)	41°03' S; 62°48' W

Neohelice granulata was formally described, illustrated and named as *Chasmagnathus granulatus* by Dana (1851, 1852) based on specimens collected on "marshes of Lake Peteninga, near Rio [de] Janeiro, Brazil" by the United States Exploring Expedition during the years 1838-1842 under the command of Charles Wilkes (Fig. 1.1 and 1.2). The type specimen was lost (Rathbun 1918).

CHASMAGNATHUS GRANULATUS.

Carapax valde convexus, sat areolatus, fronte sinuato, medio depresso et juxta marginem minutè apiculato, margine antero-laterali tenui, 2-inciso, dentibus triangulatis, acutis. Margo epistomatis inferior fronte prominentior. Pedes antici maris *crassi, subæqui, granulati, carpo intus acuto, manu supra tenui et paulo obtusâ. Pedes postici valde compressi, articulis 4to 5toque dorso paulo tomentosis, 5to pedis 2di infra non tomentoso, tarso tenui, tenuiter sulcato et sulcis hirsuto. Abdomen* maris *lateribus fere rectum.*

Carapax very convex and considerably areolate; front arcuate, slightly excavate at middle, and having a minute point on the surface; antero-lateral with two incisions. Posterior margin of epistome more projecting than the front. Anterior feet of male stout, subequal, granulate, carpus acute within, upper margin of hand a little obtuse. Posterior feet much compressed, fourth and fifth joints somewhat tomentose along the back, tarsus slender and fine sulcate, with a range of short hairs on the sulci. Sides of abdomen nearly straight and regularly convergent.

Plate 23, fig. 6 *a*, male, natural size; *b*, under view, enlarged two diameters; *c*, male abdomen and sternum, natural size; *d*, hand, natural size.

Marshes of Lake Peteninga, near Rio Janeiro, Brazil.

Figure 1.1. Facsimile of part of page 364 of Dana (1852) comprising the original description of *Neohelice granulata*.

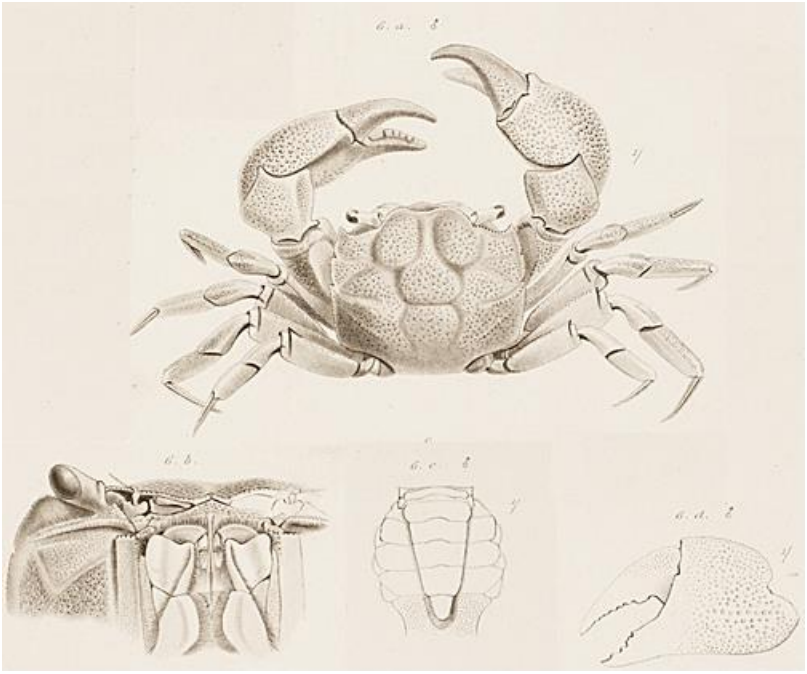

Figure 1.2. Part of plate 23 of Dana (1852), modified to show the original drawings of *Neohelice granulata* (figures 6 a-d).

The description of *N. granulata* was then reproduced by H. Milne Edwards (1853) in his "Mémoire sur la famille des *Ocypodiens*". During the following fifty years, the species was collected and mentioned as follows:

- Rio de Janeiro (Brazil). One male, collected in 1857 during the "Novara Expedition", an Austrian-Hungarian Empire expedition around the world, identified and described by Heller (1865), under the name *Helice cranulata* (sic).
- Rio Grande do Sul (Brazil). The material collected by Captain Harrington in 1859 and deposited in the Peabody Academy of Sciences (now Yale Peabody Museum), was identified by Smith (1869) as *Helice granulata* (*Chasmagnathus granulatus*). Four samples (13 specimens) from Rio Grande and another crab collected by F. Müller at "Florianopolis (Desterro)" (Brazil) in the

same year are deposited in the Museum of Comparative Zoology of Harvard University (MCZ)

- Rio Grande do Sul (Brazil). Four specimens were collected in brackish waters by Reinhold Friedrich Hensel, who was commissioned by the Berliner Akademie to conduct zoological studies in southern Brazil, from 1863 to 1866. They were described by von Martens (1869) as *Helice granulata*.
- Rio de Janeiro (Brazil). One specimen was collected during the Thayer Expedition to Brazil (1865-1866), organized by Louis Agassiz, and deposited in MCZ. The seven specimens collected at Maldonado (Uruguay) by Thomas G. Cary (Agassiz's brother-in-law) and also deposited in MCZ, were probably found during the same expedition.
- Port San Antonio and San Matías Bay (Argentina). Five specimens were collected during the Hassler Expedition, the second expedition to South America by Louis Agassiz in 1872 and deposited in the MCZ.
- Rio de Janeiro and Rio Grande do Sul (Brazil). The crabs collected by the Wilkes Expedition (1838) and by Capt. Harrington (1859), were also mentioned and briefly described by Kingsley (1880).
- Montevideo (Uruguay). Three males, “in somewhat mutilated condition, were collected at Rat Island, Monte Video (sic)” in 1878, during a two-year hydrographic survey of the Strait of Magellan by the H.M.S. "Alert", commanded by Captain George S. Nares. Later, they were identified by Miers (1881) as *Chasmognathus granulatus* (sic). Rat Island is now known as Isla Libertad.
- Montevideo (Uruguay). The material collected in 1885-7 during the “Albatross Expedition”, a circum-American journey of the U. S. Fish Commission Steamer Albatross, was studied by Rathbun (1899), referring to it as *Chasmagnathus granulatus*.
- Rio Grande do Sul (Brazil). One male and one female collected by G. Schneider in 1888 were studied by Ortmann (1894) and identified as *Chasmagnathus granulatus*.
- Rio de Janeiro (Brazil). Live crabs were observed by Moreira (1901) in Mauá and Lagoa Maricá.

Systematics

Rathbun (1918) gave a detailed description of this species based on specimens from Brazil and Uruguay under the name of *Chasmagnathus granulata*. In this monographic study of the grapsoid crabs of America, she also specified that the range of this species reached "San Matías Bay, Patagonia" based on material deposited in the Museum of Comparative Zoology of Harvard University, even if she did not examine the crabs from there (Rathbun, 1918:330).

Despite the disagreement in gender between the genus and species names introduced by Rathbun (1918), the species from then on continued to be referred to as *C. granulata* during most of the 20th century (e.g. Boschi 1964). However, some authors used *C. granulatus* (e.g. Lozada et al. 1988), and this became the most commonly used name at the end of the 20th and the early 21st centuries.

The genus *Chasmagnathus* was erected by De Haan (1833), and the type species is *C. convexus* De Haan (1833) from Japan and China. It was originally included in the subfamily Sesarminae Dana (1851) within the family Grapsidae MacLeay, 1838 (see Dana, 1851).

The Grapsidae used to be subdivided into four subfamilies: Grapsinae, MacLeay, 1838; Plagusiinae Dana, 1851; Sesarminae Dana, 1851; and Varuninae H. Milne Edwards, 1853. This taxonomic classification was adopted in systematic reviews and monographs of this family, and the classification of grapsid genera within these four subfamilies also remained unchanged and was rarely questioned until the end of the 20th century (see Schubart et al. 2000).

Originally, characters used to distinguish the four grapsid subfamilies were solely based on adult morphology, some of them being defined ambiguously or based upon possibly plesiomorphic or convergent characters (Schubart et al. 2000). Studies of comparative larval morphology showed diagnostic characters for Grapsinae, but variable setation patterns within the other three subfamilies. Diagnostic larval characters for Sesarminae, Varuninae, and Plagusiinae could only be defined if some genera were reclassified (Cuesta and Schubart 1997, Schubart and Cuesta 1998, Cuesta et al. 2001). In addition, phylogenetic relationships within all gecarcinid and grapsid crab genera reported from continental America were established based on DNA sequences of the mitochondrial large subunit ribosomal RNA (16S rRNA) gene (Schubart et al. 2000). Following comparative studies of adult and larval morphology, and the new molecular phylogenetic results, Schubart et al. (2002) proposed a new classification of grapsoid crabs (Table 1.2) that

was incorporated in the "Updated classification of the recent Crustacea" by Martin and Davis (2002) and later in the "Systema Brachyurorum" by Ng et al. (2008) and in the "Treatise on Zoology: The Crustacea" by Davie et al. (2015).

Table 1.2. Revised classification of grapsoid crabs, according to Davie et al. (2015).

Superfamily Grapsoidea MacLeay,1838
Family Gecarcinidae MacLeay 1838
Family Glyptograpsidae Schubart, Cuesta and Felder 2002 (2001 in Martin and Davis 2002).
Family Grapsidae MacLeay 1838
Family Percnidae Števčić 2005
Family Plagusiidae Dana 1851
Family Sesarmidae Dana 1851
Family Varunidae H. Milne Edwards 1853
Family Xenograpsidae Ng, Davie, Schubart and Ng 2007

The molecular phylogenies revealed that *Chasmagnathus*, *Tetragrapsus*, *Gaetice*, *Hemigrapsus*, *Cyclograpsus*, *Cyrtograpsus* and *Eriocheir* form a consistently grouped clade (Schubart et al. 2000) and that *Neohelice granulata* is most closely related to other crabs formerly included within the Sesarminae (*Metaplax elegans*, *Cyclograpsus integer*, *Helograpsus haswellianus*, *Helice crassa*, *Paragrapsus laevis*), and to others always classified within the Varuninae (*Eriocheir sinensis*, *Varuna litterata*, *Cyrtograpsus affinis*, *Hemigrapsus oregonenis* and *Brachynotus atlanticus* (see Schubart et al. 2002). Based on these molecular evidences and larval morphology (see Cuesta et al. 2001, 2002), *N. granulata* was therefore placed in the family Varunidae.

Shortly later, the taxonomic classification of the species experienced further changes. Guinot and Cleva (2002) anticipated that the species known as *Chasmagnathus granulatus* would be designated as the type species of the genus *Neohelice* Sakai, Türkay and Yang 2001 and thus renamed as *Neohelice granulata*, although they did not include a reference of the mentioned paper by Sakai and colleagues. In fact, only at the end of 2006 the foretold paper was officially published. Sakai, Türkay and Yang (2006) revised and reclassified all species formerly attributed to the genera *Helice* and *Chasmagnathus* (the so-called "*Helice*/*Chasmagnathus* complex"), redefined both genera that are now restricted to species from East Asia, and introduced new genera for the species from South America