
An Update on Reproduction in Ghost Shrimps (Decapoda: Axiidea) and Mud Lobsters (Decapoda: Gebiidea)

Patricio Hernáez

Additional information is available at the end of the chapter

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Abstract

In this report, I review the taxonomic history, body adaptations, ecology, and reproduction of the infraorders Axiidea (ghost shrimps) and Gebiidea (mud lobsters). Known until recently as the “Thalassinidea,” modern classification divided Axiidea into six families and Gebiidea into five. Ghost shrimps are characterized by having the first and second pereopod chelate and a soft and delicate body, whereas mud lobsters possess the first pereopod chelate or subchelate and second pereopod subchelate or simple with a hard and heavily calcified body. Among the main body adaptations of these organisms are distinguished: (i) carapace laterally compressed, (ii) pleon longer than the cephalothorax in ghost shrimps but usually shorter in mud lobsters, and (iii) anterior feet thrown directly forward. Current accounting of axiideans and gebiideans reaches around 781 and 240 extant species, respectively, with major number of species in Callianassidae and Upogebiidae within of each clade. Male reproductive system involves paired testes linked to the vas deferens that open in gonopores on the ventral coxal segment of the fifth pereopod. In females, the reproductive system is composed of paired and colored ovaries, one ovary shorter than another, and a pair of short and translucent oviducts linking each ovary to the gonopore, this latter located on the ventral coxal of the third pereopod. When present in males, the first pleopod is sexually dimorphic. Most ghost shrimps show distinct sexual dimorphism in body size and the major cheliped which become them in a promising group for growth studies. Hypertrophied chelipeds in males are often used to defend galleries against invasion from other shrimps from the same or opposite sex or during the intense male-to-male competition for sexual partners. Knowledge about sexual systems of these species remains limited; however, available information suggests that hermaphroditism might be commonly present in axiideans and gebiideans. Regarding mating systems, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous. Finally, considerable variability among Axiidea and Gebiidea species in fecundity and egg size may indicate important differences in the reproductive strategy and may also reflect a latitudinal trend as observed in other decapods.

Keywords: Thalassinidea, taxonomy, ecology, sexual systems, mating systems, sexual dimorphism

1. Taxonomic origin of Thalassinidea

The term “Thalassinoides” is introduced for the first time into subsection Macrura (reptant) by the zoologist Latreille [1], including in it the genera *Gebia* Leach, 1816; *Thalassinia* Latreille, 1806; *Callianassa* Leach, 1814; and *Axius* Leach, 1815. Next, this term is Latinized as Thalassinidea Latreille, 1831, incorporating it to the suborder Pleocyemata Burkenroad, 1963. Dana [2] divided Thalassinidea into Eubranchiata (species with thoracic branchiae) and Anomobranchiata (species with abdominal branchial appendages), classifying the taxa Gebidae; Callianassidae Dana, 1852; and Thalassinidea Latreille, 1831, into Eubranchiata and *Callianidea* H. Milne Edwards, 1837, and *Isaea* H. Milne Edwards, 1830, into Anomobranchiata. The famous zoologist de Saint Laurent [3] elevated the genus *Upogebia* Leach, 1814 (e.g., Callianassidae) to family rank, and she reorganized the families Callianassidae; Callianideidae Kossmann, 1880; and Axiidae Huxley, 1879, into superfamily Axioidea [4]. In another work published in the same year, she divided Reptantia into 10 groups that in her opinion were caused by the process called “radiation Triassique” [5]. In her work, she stated that infraorder Thalassinidea was the only group of Reptantia impossible to define precisely and so introduced the term (French) “Thalassinacea.” De Saint Laurent [5] argued that in “Thalassinacea,” relationship between the epistome and the carapace varied notably from one family to another, also the number of chelate pereopods (sometimes one and sometimes two); an appendix interna was not always present. From these observations, she proposed the separation of “Thalassinacea” into infraorders Axiidea and Gebiidea, thus transferring the families Axiidae and Callianassidae for the former infraorder and Laomediidae; Upogebiidae Borradaile, 1903; and Thalassinidea for the latter infraorder [5].

The first cladistic analysis of Thalassinidea was conducted by Poore [6]. He found the group to be monophyletic and divided into three superfamilies (Callianassoidea, Axioidea, Thalassinidea). A subsequent phylogenetic study using molecular data divided Thalassinidea into two major clades [7]. The first clade composed of the families Strahlaxiidae Poore, 1994, and Callianassidae and the second clade of Laomediidae Borradaile, 1903, Upogebiidae, and Thalassinidea (see also [8] sperm data; [9] molecular data). Sakai [10] compared the gastric mill in species of the Thalassinidea and found the group “diphyletic.” From his information, he proposed the division of Thalassinidea into superorder Callianassoidea composed of five families (Axiidae; Callianassidae; Callianideidae; Ctenochelidae Manning and Felder, 1991; Gourretiidae Sakai, 1999) and Thalassinidea composed of three families (Laomediidae, Upogebiidae, Thalassinidea). In the former group, all species are characterized by the presence of a propyloric ossicle simple, whereas in the latter group by having a propyloric ossicle triangularly protruded downward [6]. Lastly, Robles et al. [11] undertook a molecular phylogeny of the thalassinideans and discovered the same two groups proposed by de Saint Laurent [4, 5] and other researchers [12–14].

Taxon

Class Malacostraca

Subclass Phyllocarida

Subclass Hoplocarida

Subclass Eumalacostraca

Superorder Syncarida Packard, 1885

Superorder Peracarida Calman, 1904

Superorder Eucarida Calman, 1904

Order Euphausiacea Dana, 1852

Order Decapoda Latreille, 1802

Suborder Dendrobranchiata Spence Bate, 1888

Suborder Pleocyemata Burkenroad, 1963

Infraorder Achelata Scholtz and Richter, 1995

Infraorder Anomura MacLeay, 1838

Infraorder Astacidea Latreille, 1802

Infraorder Axiidea de Saint Laurent, 1979

Family Axiidae Huxley, 1879

Family Callianassidae Dana, 1852

Family Callianideidae Kossmann, 1880

Family Gourretiidae Sakai, 1999

Family Micheleidae Sakai, 1992

Family Strahlaxiidae Poore, 1994

Infraorder Brachyura Latreille, 1802

Infraorder Caridea Dana, 1852

Infraorder Gebiidea de Saint Laurent, 1979

Family Axianassidae Schmitt, 1924

Family Kuwaitupogebiidae Sakai, Turkey and Al Aidaroos, 2015

Family Laomediidae Borradaile, 1903

Family Thalassinidea Latreille, 1831

Family Upogebiidae Borradaile, 1903

Infraorder Glypheidea Van Straelen, 1925

Infraorder Polychelida Scholtz and Richter, 1995

Infraorder Procarididea Felgenhauer and Abele, 1983

Infraorder Stenopodidea Spence Bate, 1888

Table 1. Families of Axiidea and Gebiidea within the classification of the arthropod superclass Multicrustacea based on Dworschak et al. [15], updated by worms [22].

Currently, it is reasonably assumed by researchers that Axiidea and Gebiidea represent two distinctly separate infraorders of decapods whose main evolutionary characteristic is the fossorial lifestyle [15]. Members of Axiidea (casually known as ghost shrimps) are characterized by having the first and second pereiopod chelate and a soft and delicate body, whereas all Gebiidea (casually known as mud lobsters) possess the first pereiopod chelate or subchelate and second pereiopod subchelate or simple with a hard and heavily calcified body [15, 16]. Recent discovery of new species has added a series of new families within Axiidea and Gebiidea [17, 18]. Considering this information, modern classification of both groups divided Axiidea into six families and Gebiidea into five (Table 1). Nevertheless, taxonomy of old name Thalassinidea follows being very controversial among carcinologists from the “American school” and opinions of Sakai, particularly in what concerns to the correct use of the names Axiidea and Gebiidea versus Callianassidea and Thalassinidea [19, 20].

2. A body adapted for a fossorial lifestyle

In order to understand and define what is meant by ghost shrimp and mud lobster, the general morphological components of the infraorders Axiidea and Gebiidea need to be examined.

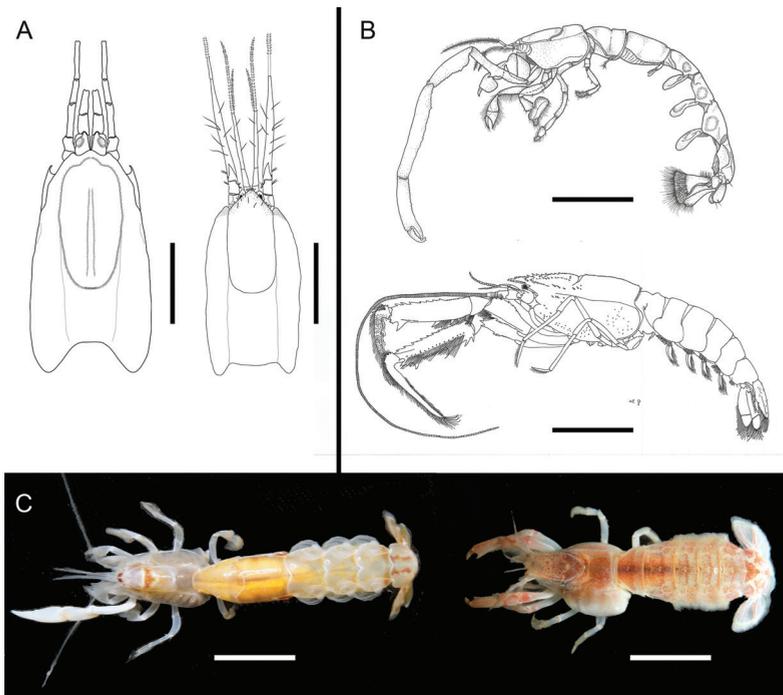


Figure 1. Main morphological adaptations in Axiidea and Gebiidea. (A) Carapace of *Neocallichirus grandimana* (left panel) and *Axianassa linda* (right panel), dorsal view; (B) male specimen of *Callichirus seilacheri* (top panel) and *Naushonia macginitiei* (Glassel, 1938) (down panel), lateral view; (C) male specimen of *Lepidophthalmus siriboia* (left panel) and *Upogebia omisssa* (right panel), dorsal view. (a,B) left and right panel, scale bar = 1 cm, 0.5 cm, respectively; (B) top and down panels, scale bar = 1 cm, 0.5 cm, respectively.

The carapace in most of these species (except in laomediids of the genus *Naushonia*) is laterally compressed and can be strongly ornamented (**Figure 1A**, left and right panel), with spines and tubercles as in Thalassinidea and Upogebiidae (Gebiidea) or unornamented as in Callianassidae and Callianideidae (Axiidea) [15, 16]. The pleon is longer than the cephalothorax in most ghost shrimps (**Figure 1B**, top panel) but usually shorter in mud lobsters (**Figure 1B**, down panel), and anterior feet are thrown directly forward in all members of these clades [15, 16] (**Figure 1C**, left and right panel).

3. Diversity and ecological importance

Inhabiting most oceans and seas of the world, ghost shrimps (Axiidea) and mud lobsters (Gebiidea) exhibit a greatest diversity with about 423 and 192 extant species, respectively [21]. According to information available in database World Register Marine Species, for Axiidea and Gebiidea, those values have increased in about 85% and 25%, respectively, during the last decade [22]. In terms of extant species, family Callianassidae exhibits the greatest diversity within infraorder Axiidea whereas Upogebiidae within Gebiidea (**Table 2**).

Both axiideans and gebiideans are known for constructing burrows of different shapes and depths [23–27] (**Figure 2A**) and for playing an important role in shaping the community structure in intertidal and shallow water of marine habitats [28–31]. Bioperturbation produced by these organisms, i.e., the activity of water and sediment expulsion from the galleries, contributes to the suspension of organic matter, nitrogen fixation, and the increases of food availability among the trophic levels [32–34] (**Figure 2B**). Members of Axiidea and Gebiidea can be found inhabiting as sponge symbionts, living between coarse coral rubble or even associated to hydrocarbon seeps

Taxon	Number of genera	Extant species
Infraorder Axiidea		
Family Axiidae	63	205
Family Callianassidae	67	495
Family Callianideidae	6	18
Family Gourretiidae	9	20
Family Micheleidae	4	33
Family Strahlaxiidae	3	10
Infraorder Gebiidea		
Family Axianassidae	2	15
Family Kuwaitupogebiidae	1	1
Family Laomediidae	4	21
Family Thalassinidea	1	11
Family Upogebiidae	13	192

Table 2. Number of genera and species for each family of Axiidea and Gebiidea based on database of worms [22].

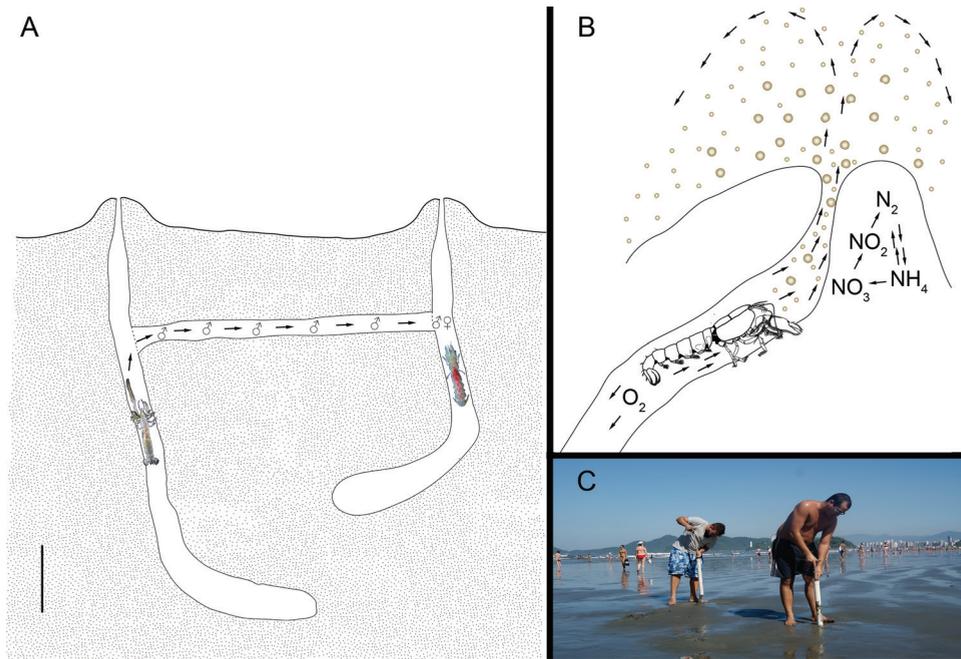


Figure 2. (A) Burrow morphology and copulatory behaviour in *Callichirus seilacheri* (Callianassidae), scale bar = 20 cm; (B) model of bioperturbation activity in *Axianassa linda* (Axianassidae); (C) fishermen harvesting *Callichirus major* (Callianassidae) at São Paulo State, Brazil.

and hydrothermal vents in deep water [35–38]. Some species of ghost shrimps are considered ecosystem engineers because of their capacity to modify, maintain, and/or create habitats for other marine invertebrates [39–40]. Also, several ghost shrimps and mud lobsters are used as a bait for recreational fishing and human consumption [41–45] (**Figure 2C**).

Dworschak et al. [15] stated that most ghost shrimps and mud lobster species are characterized by solitary habits; however, such assumption lacks empirical support from the available literature. With the exception of larval period [46–49], axiideans and gebiideans spend their lifetime within of gallery [15], which makes it difficult to capture and study them. As a result, the knowledge about population dynamics and reproduction of these species is restricted to about 6.00% of already described species, being most of these studies realized in species of the families Callianassidae and Upogebiidae [40, 50–56].

4. Reproductive biology

4.1. Gonopores and primary sexual characters

The location of the male and female sexual openings in Axiidea and Gebiidea is similar to described universally for the reptant decapods [57]. Males possess prominent gonopores on

the ventral coxal segment of the fifth pereopod, whereas females have oval gonopores on the ventral coxal segment of the third pereopod [40, 58, 59] (**Figure 3A**).

Information about internal anatomy of the reproductive system is virtually nonexistent in most species of ghost shrimps and mud lobsters. Scarce information published point out that male reproductive system involves paired testes dorsally to the hepatopancreas and the intestine and is located between first and second abdominal somites, whose connection with genital openings (gonopores) is produced through a pair of translucent or whitish vas deferens [60] (**Figure 3B**). Secreting epithelium of the vas deferens is responsible for forming the gelatinous spermatophoric mass [61], as observed in other decapods [62]. Female sexual system is composed of paired orange or dark red ovaries (depending upon developmental stage), one ovary shorter than another, both visible through pleonal region and a pair of short and translucent oviducts linking the ovary to gonopore [59, 60] (**Figure 3C**). Seminal receptacle or spermathecae have not been described for any Axiidea and Gebiidea, despite attempts to find them [63]. Laboratory observations show that females of callianassid shrimps are not able to store sperm [64], as reported in most brachyuran crabs [65].

4.2. Secondary sexual characters

Males of most ghost shrimps and mud lobsters can be identified by the absence/presence and morphology of the first pleopod. The first pleopod is absent in most males of Axianassidae, Laomediidae, Strahlaxiidae, and Upogebiidae and in numerous Callianassidae [15, 16, 66, 67]. When present, the male first pleopod is uniramous and can be unsegmented as in *Thalassina* [68], bisegmented as in *Callichirus* [58], or composed of four articles as in *Ctenocheles* [69]. Male first pleopod in some species as *Callianidea mariamartae* Hernáez and Vargas, 2013, and *Marcusiarius lemoscastroi* Rodrigues and de Carvalho, 1972, is morphologically similar to gonopods of *Brachyura* [70, 71], showing a tiny size and function totally unknown [15]. First pleopod plays an important role during the mating behavior of caridean shrimps [72] and brachyuran crabs [65]; however, their function is not clearly defined in Axiidea and Gebiidea.

Female first pleopod is present in all females of Axiidea and Gebiidea [15]. It is uniramous and consists of one article in Axianassidae, two articles in most families, or three articles in Callianassidae, with the distal part sometimes appearing as a shovel (Callianassidae) or flagellum (Laomediidae, Callianideidae) [58, 59, 66, 73]. Depending upon species, sometimes the first two pairs or all female pleopods are used for carrying the eggs during the incubation of embryos [55, 74–76]. Females use pleopods 3–5 to generate strong water currents during the spawning and so help the larvae release from the burrow [76].

Ghost shrimps constitute a promising group for growth studies because many of them show marked differences between relative growth of chelipeds of males and females during post-puberty phase. In Callianideidae and Callianassidae, for instance, males show a positive allometric growth of the major cheliped in relation to body size, whereas this morphometric relationship is isometric in females of both families [40, 77]. According to Rodrigues and Höld [78], hypertrophied chelipeds in males of ghost shrimps are often used to defend galleries against invasion from other shrimps from the same or opposite sex. Also, Felder and Lovett [51] suggest that antagonistic interactions among males of callianassid shrimps might cause

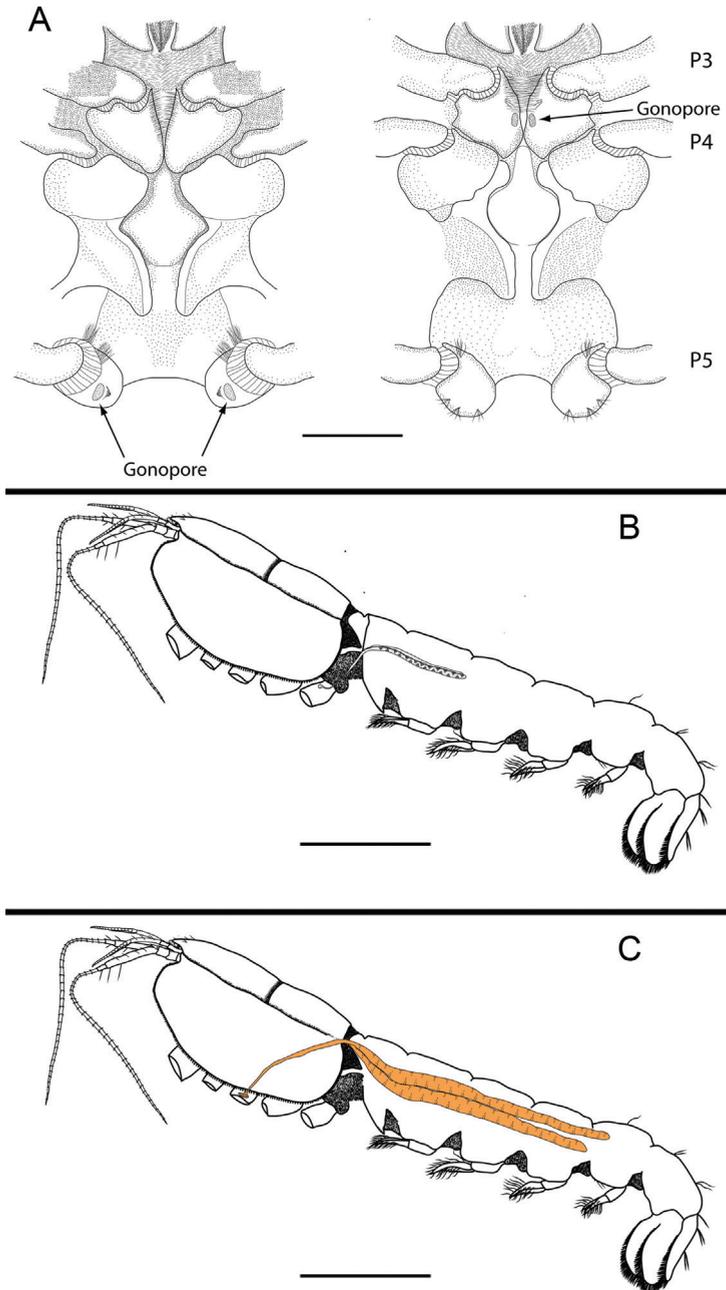


Figure 3. Schematic representation of the external genitalia and reproductive system in males (A, left panel, B) and females (A, right panel, C) of ghost shrimps and mud lobster. A–C scale bar = 5 mm.

a high mortality of adult males, thus creating a bias toward females in these populations. Consequently, development of extremely larger chelipeds in callianassid species not only includes morphometric changes during sexual maturity but also can provide some advantages to males, a competition for sexual partners, as were widely documented in several species of Caridea Dana, 1852 [72].

4.3. Sexual systems

Sexual system varies considerably in Decapoda. Most caridean shrimps and brachyuran crabs are gonochoric, that is, all individuals in the population exhibit separate sexes throughout their lifetime [65, 72]. Other species are sequential hermaphrodites in which the individual changes sex at some point in the life history [79–84]. If the initial sex is male, the condition is known as protandry; the converse situation is protogyny [85]. Finally, several species have been reported as simultaneous hermaphrodites sensu Ghiselin [86], that is, an organism has both male and female sexual organs at the same time [72, 87, 88].

While the sexual system of most groups of Decapoda is well known such as Caridea [72], Astacidea [89], Anomura [90], and Brachyura [65] for most axiideans and gebiideans, the distribution of the sexes among individuals is not clear. This is because many researchers have omitted to report explicitly the sexual system of their focus species, wrongly accepting that most ghost shrimps and mud lobsters are gonochoric. Secondly, because in ghost shrimp and mud lobster studies, the sex ratio as a function of size is rarely reported, which is crucial to determine any sex changing through the ontogeny of one species [91].

Several studies conducted in Axiidea and Gebiidea species have reported morphological evidences that aim for a sexual system more complex than simply the existence of separate sexes during the lifetime of these species. For instance, in the intertidal mud lobster *Upogebia major* (De Haan, 1841) (Upogebiidae) and in the ghost shrimp *Callinectes major* (Say, 1818) (Callianassidae), male has the gonad divided in a posterior ovarian section and an anterior testicular section [92, 61] (**Table 3**). In both species, ovarian section produces functional oocytes. In other species of ghost shrimps and mud lobsters have been reported specimens with male and female gonopores which have been classified as intersexed (**Table 3**). To summarize, for 21 species of Axiidea and 12 of Gebiidea, explicit information—or strong indirect evidence—on their sexual system was available. Of these, 26 species are gonochoristic (i.e., all individuals in the population exhibit separate sexes throughout their lifetime); 2 males are hermaphrodites, and 10 species present intersexed specimens (**Table 3**). Considering this information and given that reproductive biology has been studied in only a small proportion of the 781 ghost shrimps and 240 mud lobsters, it can be concluded that hermaphroditism might not be unusual in these organisms.

4.4. Mating systems

Overall, monogamous decapods usually live in heterosexual pairs as a form to ensure the mating and optimize the survival [93]. In most monogamous species, disproportionate sexual dimorphism

Taxon	Sexual system	Intersex	Reference
Axiidea			
Callianassidae			
<i>Biffarius filholi</i> (A. Milne-Edwards, 1878)	Gc		[54]
<i>Callianassa aqabaensis</i> Dworschak, 2003		I (M,F)	[116]
<i>Callianassa subterranea</i> (Montagu, 1808)	Gc		[117]
<i>Callichirus garthi</i> (Retamal, 1975)	Gc	I (F)	[40]
<i>Callichirus islagrande</i> (Schmitt, 1935)	Gc		[63]
<i>Callichirus major</i> (Say, 1818)	H (M)	I (F)	[100]
<i>Callichirus seilacheri</i> (Bott, 1955)	Gc	I (F)	P. Hernandez unpublished data
<i>Lepidophthalmus bocourti</i> (A. Milne-Edwards, 1870)	Gc		P. Hernandez unpublished data
<i>Lepidophthalmus louisianensis</i> (Schmitt, 1935)	Gc		[51]
<i>Lepidophthalmus sinuensis</i> Lemaitre and Rodrigues, 1991	Gc		[118]
<i>Lepidophthalmus siriboia</i> Felder and Rodrigues, 1993	Gc		[56]
<i>Neocallichirus maryae</i> Karasawa, 2004	Gc		P. Hernandez unpublished data
<i>Neocallichirus nickellae</i> Manning, 1993	Gc		P. Hernandez unpublished data
<i>Neotrypaea californiensis</i> (Dana, 1854)	Gc		[119]
<i>Neotrypaea tabogensis</i> (Sakai, 2005)	Gc		P. Hernandez unpublished data
<i>Nihonotrypaea harmandi</i> (Bouvier, 1901)	Gc		[120]
<i>Nihonotrypaea japonica</i> (Ortmann, 1891)	Gc		[53]
<i>Nihonotrypaea petalura</i> (Stimpson, 1860)	Gc		[120]
<i>Sergio mirim</i> (Rodrigues, 1966)	Gc		[121]
<i>Sergio trilobata</i> (Biffar, 1970)	Gc		[122]
Callianideidae			
<i>Callianidea mariamartae</i> Hernandez and Vargas, 2013	Gc		[70]
Gebiidea			
Axianassidae			
<i>Axianassa australis</i> Rodrigues and Shimizu, 1992	Gc		P. Hernandez unpublished data
Upogebiidae			
<i>Austinogebia edulis</i> (Ngoc-Ho & Chan, 1992)		I (M)	[123]
<i>Austinogebia spinifrons</i> (Haswell, 1882)		I (F)	[124]
<i>Paragebicula edentata</i> (Lin, Ngoc-Ho & Chan, 2001)		I (M)	[125]
<i>Upogebia dawsoni</i> Williams, 1986	Gc		[126]
<i>Upogebia deltaura</i> (Leach, 1816)		I (M)	[50]

Taxon	Sexual system	Intersex	Reference
<i>Upogebia major</i> (De Haan, 1841)	H (M)		[92]
<i>Upogebia omissa</i> Gomes Corrêa, 1968	Gc		P. Hernandez unpublished data
<i>Upogebia pusilla</i> (Petagna, 1792)	Gc		[127]
<i>Upogebia stellata</i> (Montagu, 1808)	Gc	I ()	[128]
<i>Upogebia thistlei</i> Williams, 1986	Gc	I (M)	[129]
<i>Upogebia vasquezi</i> Ngoc-Ho, 1989	Gc		[130]

Table 3. Probable sexual system and the presence of specimens intersexed in 21 ghost shrimps and 12 mud lobsters. Empty spaces are left where no information is available; (Gc) = gonochoristic, (H) = hermaphroditic, (I) = intersex, (M) = male, and (F) = female.

of chelipeds is not observed because sexual selection is weak given that monogamy evolved from fidelity between heterosexual pairs [94]. On the contrary, in polygamous species there is no fidelity among individuals of the opposite sex, wherefore agonistic encounters are common between adult males during the search for receptive females [72, 95]. In these species, males invest heavily in structures, such as chelipeds, that are used as armament against other potential competitors [96, 97]. Considering this information, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous.

In the intertidal ghost shrimp *Callichirus seilacheri* (Bott, 1955), the burrow is individually inhabited by one male or a female (**Figure 2A**), and adult male develops hypertrophied chelipeds which is a potential evidence of intense male-to-male competition for sexual partners and therefore an indirect evidence of polygamy [98]. In a study conducted in *Callichirus isla-grande* (Schmitt, 1935), an intertidal species in that males possess highly developed chelipeds [59], the egg mass of females is fertilized by multiple males which denotes polyandry [63]. In both species, the authors assume that mating occurs when the male digs a straight and almost horizontal connection from its gallery to other nearby galleries in search of a receptive female (**Figure 2A**), such as one that is observed in *Upogebia noronhensis* Fausto-Filho, 1969 [98]. Unfortunately, information about mating system in Axiidea and Gebiidea is virtually nonexistent. Further studies including behavioral experiments between male and female specimens should be carried out to investigate a possible mating system in these species.

4.5. Sexual dimorphism in body size

In general, females of ghost shrimps attain, in average, a larger body size than males such as *Biffarius filholi* (A. Milne-Edwards, 1878) [99], *C. major* [100], and *Lepidophthalmus siriboia* Felder and Rodrigues, 1993 [56]. Females usually invest more energy into somatic growth than males when their reproductive success depends on reaching a larger body size [101]. In decapods, such evolutionary trend is explained by the fact that fecundity in females increases with body size [74, 102–105]. Supporting this assumption, fecundity in species of callianassids increase with the female size, resulting in greater production of eggs in larger females [54, 74, 75].

4.6. Egg number and egg size

The considerable variability among Axiidea and Gebiidea species in view of fecundity and egg size (**Table 4**) may indicate important differences in the reproductive strategy and may also reflect a latitudinal trend, as was observed in other decapods [106–110]. In *C. seilacheri*, for instance, females produce the highest number of eggs compared to those axiideans and gebiideans where data are available. However, this ghost shrimp and mud lobsters are the largest species among those listed in **Table 4**, and it is assumed that the area available for egg attachment increases with female size [102, 111]. When compared to a similar-sized species *Upogebia deltaura* (Leach, 1816) (18.9 mm CL, 5304 eggs) [50], fecundity in *C. seilacheri* is still substantially higher (18.6 mm CL, 9612 eggs). Moreover, this species produces considerably larger eggs (0.884 mm) than *U. deltaura* (0.558 mm). It is speculated that these differences in egg numbers in similar-sized species are related to the elasticity of the abdomen, which provides more space for egg attachment.

Egg size is one of the most variable parameters in decapods and offers valuable information on a species' reproductive strategy. It is a useful indicator of the duration of embryogenesis and larval size at hatching [112]. Moreover, several studies on ghost shrimps and mud lobsters showed a clear relation between egg size and type of larval development [113–115]. Such information, however, is restricted to just a few species of both clades.

Taxon	Carapace length (mm)	Number of eggs	Egg length (mm)	Reference
Infraorder Axiidea				
Family Callinassidae				
<i>Biffarius filholi</i>	5.5–14.9	1985	0.68	[54]
<i>Callichirus garthi</i>	18.6–23.2	17,450	0.88	[40]
<i>Callichirus kraussi</i> (Stebbing, 1900)	n.a.	122	1.52	[113]
<i>Callichirus major</i> (Brazil)	10.3–15.0	4564	0.79 ^a	[75]
<i>Callichirus seilacheri</i>	12.2–17.2	2387	0.71	P. Hernáez unpublished data
<i>Lepidophthalmus louisianensis</i>	n.a.	598	n.a.	[47]
<i>Lepidophthalmus sinuensis</i>	7.0–16.8	251	1.22	[118]
<i>Pestarella tyrrhena</i> (Petagna, 1792)	5.2–10.4 ^b	270	1.18	[131]
Infraorder Gebiidea				
Family Upogebiidae				
<i>Upogebia affinis</i> (Say, 1818)	n.a.	10,000	n.a.	[132]
<i>Upogebia deltaura</i>	16.6–18.9	4757	0.56	[50]
<i>Upogebia pusilla</i>	14.7–16.6	n.a.	n.a.	[127]

n.a., information not available. Letter in superscript indicates information obtained from further estimation

Table 4. Carapace length of ovigerous females and number and length of eggs in some ghost shrimp and mud lobster species.

5. Conclusion

An updated classification of the infraorders Axiidea (ghost shrimps) and Gebiidea (mud lobsters) divide each of these clades into six families and five families, respectively. However, controversial taxonomic history of these infraorders is far from over due to recent discovery of new taxa. Diagnostic features of these organisms mainly include (i) carapace laterally compressed, (ii) pleon longer than the cephalothorax in Axiidea but usually shorter in Gebiidea, and (iii) anterior feet thrown directly forward. A recent count estimates the diversity of Axiidea and Gebiidea in about 781 and 240 extant species, respectively. In general, information about reproduction of these organisms is virtually nonexistent. Scarce reports about external and internal genital apparatus show that male possesses gonopores on the ventral coxal segment of the fifth pereopod whereas females on the ventral coxal segment of the third pereopod. Males of most ghost shrimps and mud lobsters can be identified by the absence/presence and morphology of the first pleopod and sexual dimorphism in the major cheliped during post-puberty phase. According to available information, gonochorism is the sexual system most common within Axiidea and Gebiidea. However, two cases of hermaphroditism and several cases of intersexuality have been also reported in ghost shrimps and mud lobsters that would be indicating the need of further studies about this topic in these organisms. Regarding mating system, all species of ghost shrimp and mud lobster with solitary habits and remarkable sexual dimorphism in the major cheliped are expected to be polygamous. Lastly, considerable variability among Axiidea and Gebiidea species in fecundity and egg size seems to indicate important differences in the reproductive strategy of these decapods.

Author details

Patricio Hernandez^{1,2*}

*Address all correspondence to: phernaez@lycos.com

1 Universidad de Tarapaca – UTA, Facultad de Ciencias, Centro de Estudios Marinos y Limnologicos, Arica, Chile

2 Universidade Estadual Paulista – UNESP, Instituto de Biociencias – IB, Grupo de Pesquisa em Biologia de Crustaceos – CRUSTA, Campus do Litoral Paulista, Praca Infante Dom Henrique, Sao Vicente, SP, Brasil

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