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On the sexuality of South American Parastacidae (Crustacea, Decapoda)

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Summary

Ten parastacid species inhabit South American continental waters, grouped in the genera *Samastacus*, *Virilastacus* and *Parastacus*. The sexuality of these species is one of the most unknown and controversial features of their biology. This article gives updated information about these species sexuality. Information is also provided on the geographic distribution, habitat and lifestyle of each of these parastacids. Three patterns of sexuality are distinguished: (1) gonochorism, in the lake populations of *S. spinifrons* and *V. araucanius*; (2) permanent intersexuality in *P. pugnax*, *P. varicosus*, *P. pilimanus*, *P. defossus* and *P. saffordi*; and (3) partial protandric hermaphroditism in the fluvial populations of *S. spinifrons* and *P. nicoleti*. None of these patterns can be assigned to *P. laevigatus* and *P. brasiliensis* since no studies of this kind are available for *P. laevigatus*, and those conducted on *P. brasiliensis* yield contradictory results.

Key words: Decapoda, Parastacidae, South America, sexuality, geographic distribution, habitat

Introduction

Ten crayfish species of the Parastacidae family inhabit South American continental waters. Eight of them belong to *Parastacus*, one to *Samastacus* and one to *Virilastacus* (Hobbs, 1991). They are distributed in two widely separate geographical regions, southeast Brazil, Uruguay and northeast Argentina, and the center-south of Chile, including Lake Nahuel-huapi in Argentina (Riek, 1971; Manning and Hobbs, 1977; Buckup and Rossi, 1980; Hobbs, 1989).

The presence of supernumerary gonopores in *Parastacus* is known since von Martens (1869) described *Astacus pilimanus* (=*Parastacus pilimanus*) and *A. brasiliensis* (=*P. brasiliensis*). This character was later observed in *P. saffordi*, *P. varicosus*, *P. defossus* and *P. hassleri* (=*P. pugnax*) (von Ihéring, 1892; Faxon, 1898; Lönnberg, 1898; Hay, 1905; Turner, 1935). Even though these authors did not examine *P. nicoleti* specimens, other workers later assumed, without new evidence, that the existence of supernumerary gonopores was a characteristic of the genus [see diagnoses of Riek (1971) and Hobbs (1974, 1991)].

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External sexual characters are not mentioned in the descriptions of *Samastacus spinifrons* (Philippi, 1882) and *Virilastacus araucanius* (Faxon, 1914). Subsequent studies report the lack of supernumerary gonopores in *S. spinifrons* (Faxon, 1898; Lönnberg, 1898; Holthuis, 1952), and the presence of a single pair of sexual orifices per specimen, both in *S. spinifrons* (Hay, 1905) and in *V. araucanius* (Rudolph and Rivas, 1988; Martínez et al., 1994). This was interpreted by several authors as an external manifestation of gonochorism (Porter, 1904; Ringuelet, 1949; Bahamonde, 1951; Riek, 1971; Hobbs, 1974; Bocic et al., 1988; Hobbs, 1991; Rudolph and Iraçabal, 1994; Rudolph, 1995a, 1996). However, intersexual specimens of *S. spinifrons* have been recently captured in some rivers of southern Chile (Rudolph, 1999a, 1999b).

For many years the functional significance of supernumerary gonopores in these species has been poorly documented, particularly in relation to *Parastacus*, due to the low number of species and specimens analyzed and the bad conditions of preservation in the latter. To explain this phenomenon, Lönnberg (1898) and Hay (1905) postulated a rudimentary hermaphroditism, which was disputed by Turner (1935) and by Thompson (1982). This incomplete knowledge, as well as the assumption of a given type of sexuality — without the support of anatomical and histological studies of gonads and gonoducts in representative samples — have hindered better understanding the reproductive and population biology.

Nonetheless, since the 1980s, further biological studies of these species have been conducted, as well as anatomical and histological descriptions of their genitalia. The aim of the present study was to compile this information and to update the knowledge on the sexual systems of South American parastacids.

Samastacus Riek, 1971

Samastacus spinifrons *(Philippi, 1882)*

This is a slightly burrowing species found in lentic and lotic habitats, from the Aconcagua river (32°50′S, 70°59′W) to the peninsula of Taitao (46°30′S; 74°30′W) in Chile, and the lake Nahuel-huapi in Argentina. Unlike the other species of *Parastacus*, *S. spinifrons* has always been considered as gonochoric due to the presence of a single pair of gonopores per specimen (Hay, 1905; Rudolph, 1995a, 1996). Female gonopores are ellipsoidal, calcified in prepuberty females or decalcified in puberty specimens. Male gonopores are located on the apex of a tubular and calcified phallic papilla (Hobbs, 1991; Rudolph, 1996). In the specimens with female gonopores, the gonad consists of a pair of ovarian tubules and one oviduct emerging from each of them. In contrast, in the specimens with phallic papillae, the gonad is formed by two testicular tubules. A vas deferens originates from each of these tubules, adjacent to its terminal portion the androgenic gland is located (Rudolph, 1999a). Some studies, although not referring to the external sexual characters, provide information as to the morphometric relations (length–width of cephalothorax and abdomen) in males and females, sex-ratio and rate of ovigerous females. This information contributed to the consideration of the species as gonochoristic (Lönnberg, 1898; Porter, 1904; Bahamonde, 1951; Bocic et al., 1988; Rudolph and Iraçabal, 1994). These data served as a biological foundation for the diagnoses of Riek (1971) and Hobbs (1974, 1991) of *Samastacus* as gonochoric. Nonetheless, Rudolph (1995a, 1999a,1999b) has described 55 specimens with supernumerary gonopores from six fluvial populations of southern Chile. According to the number and position of their gonopores, 10 gonopore patterns were described. The anatomic and histologic analyses of their genitalia demonstrated that 34 of them were intersex males since, despite their entirely masculine gonad with its respective spermiducts and phallic papillae, they also had one or two female gonopores with respective oviducts. Thirteen of them had ovotestes with oviducts and vasa deferentia that connected the ovotestes female and male portions with the respective gonopores. The eight remaining specimens were intersex females, with entirely feminine gonads and the corresponding feminine oviducts and gonopores. Nevertheless, they also had one or two phallic papillae with respective spermiducts (see Rudolph 1995a, 1999a). Morphometric analyses of normal male and female abdomens, compared to those of intersex specimens, showed that the latter had abdomens with masculine characteristics, i.e., their abdomens are shorter, more narrow and with lower pleurae that the abdomens of the normal females (Rudolph, 1999a).

Virilastacus Hobbs, 1991

Virilastacus araucanius *(Faxon, 1914)*

For over 70 years this species has only been known by its type, a male captured in 1908 in a cascade near Corral (39°51′S; 73°24′W) in the south of Chile. Faxon (1914) considered it as a probably burrowing

species due to its laterally compressed cephalothorax. This assumption is consistent with subsequent findings. In Valdivia Jara (1983) found a male coexisting with specimens of *P. nicoleti*. Rudolph and Rivas (1988) collected a male in a marshy zone at Hualqui (36°56′S; 72°55′W) coexisting with *P. pugnax* specimens. Martínez et al. (1994) captured two males and six females at Cosmito (36°46′S; 73°01′W) in the same conditions reported by Rudolph and Rivas (1988). Their distribution ranging from Cosmito to Corral in south-central Chile.

Although there are few and brief descriptions of its sexual characters, we may deduce that this is a gonochoric species. The female has ellipsoidal gonopores, partially surrounded by pilosities and covered by a thin, slightly convex membrane. The male has an elongated and calcified phallic papilla, the longest observed in South American parastacids, in whose apical end the masculine gonopore is located (Rudolph and Rivas, 1988; Martínez et al., 1994; Hobbs, 1991). The authors of the present paper verified, through dissections performed in 21 specimens of *V. araucanius*, that the external expression of sex corresponds to the gonadal sex of each specimen. No data are available on any kind of intersexes in this species.

Parastacus, Huxley, 1879

Parastacus pugnax *(Poeppig, 1835)*

This is a markedly burrowing species inhabiting underground waters, in semi-marshy lands, between the Aconcagua River (32°50′S; 70°59′W) and Carahue (38°40′S; 73°09′W) in the Chilean central-southern region (Bahamonde and López, 1963). In these sites the individuals burrow galleries with multiple entrance tunnels converging towards a chamber at the level of underground water where it develops its entire life-cycle in groups with an apparently social lifestyle (Rudolph, 1997a).

The coexistence of male and female gonopores in this species was studied by dissections of a few individuals by Lönnberg (1898), Hay (1905) and Turner (1935). To explain this character, Lönnberg postulated rudimentary hermaphroditism which, according to Hay, would extend to the remaining *Parastacus* species (except *S. spinifrons*), a theory subsequently disputed by Turner. Rudolph (1997a) showed that both males and females of this species are intersexual by examining the sexual characters of 538 specimens captured at Nehuentúe in the south of Chile. These specimens had supernumerary gonopores and a single gonad — either testis or ovary — with respective gonoducts and gonopores. Males have well developed vasa deferentia and androgenic glands. In turn, oviducts are rudimentary and female gonopores are semi-ellipsoidal with a markedly calcified sheath. Female oviducts are well developed and gonopores are ellipsoidal, covered by a non-calcified or partly calcified membrane. In contrast, spermiducts are rudimentary and lack androgenic gland (see Rudolph, 1997a). Under 26.0 mm of standard cephalothorax length (SCL), the morphology of the female and male gonopores as well as the relative width of the abdomen and the height of the pleura were the same in all specimens, which did not allow externally distinguishing between the sexes. However, their gonads had already differentiated (60.4% of intersex males and 39.6% intersex females). At about 26.0 mm of SCL, gonadic females would undergo their puberty molt, and the female gonopores would complete their ellipsoidal shape, open to the outside and covered by a decalcified membrane to facilitate oocyte extrusion. The abdomen of these females is wider and their pleurae are also higher than in the males abdomen. These permanent secondary sexual characters of the females are associated to their eggs incubation (Rudolph, 1997a).

Parastacus varicosus *Faxon, 1898*

P. varicosus is a burrowing species which builds shallow (50-cm deep) spiraling galleries that culminate in a chamber which shelters individuals of different generations. According to Amestoy (1982), from May to July juveniles would also be found in the flooded lands surrounding their galleries. Their geographic distribution encompasses the south east region of Rio Grande do Sul in Brazil and the provinces of Rocha and Maldonado in eastern Uruguay (Hobbs, 1989; Morrone and Lopretto, 1994).

Faxon (1898) was the first to report the coexistence of female and male gonopores in specimens of *P. varicosus*. Hay (1905) confirmed such coexistence. Thompson (1982) studied the sexual characters of the species, as well as the female gonad histology. This allowed her to ratify the observations of Faxon (1898) and Hay (1905), and at the same time to verify that the gonad is completely male or female and originates two pairs of gonoducts toward the gonopores located in the coxae of the third and fifth walking legs. No testicular tissue was found in the female gonad.

Rudolph et al. (1999) analyzed the sex characters of 142 *P. varicosus* specimens and found that under 22.6 mm of SCL, the external morphology of all the

individuals studied ($n=105$) did not allow sex differentiation. However their gonads were already differentiated: 57.1% were intersex females with ovaries, oviducts and vasa deferentia, and the rest were intersex males with testicles, vasa deferentia and oviducts. Over 22.6mm SCL, the ovaries of the intersex females had oocytes in vitellogenesis, well developed oviducts and rudimentary vasa deferentia. Externally these females had ellipsoidal female gonopores, surrounded by a number of setae, with an entirely or partially decalcified sheath and a rather broad abdomen with higher pleurae than those of intersex males of the same size. These morphological features allow distinguishing between sexes in specimens of 22.6 mm SCL or larger.

Parastacus pilimanus *(von Martens, 1869)*

This is a burrowing parastacid inhabiting low, marshy lands southeast of Rio Grande do Sul in Brazil, the northeast of Argentina and eastern Uruguay (Hobbs, 1989; Morrone and Lopretto, 1994). In these areas they construct lairs with several entrance tunnels (three to seven) converging into a central one of larger diameter, which extends till reaching the phreatic layer. Individuals of different generations coexist in this central tunnel (Buckup and Rossi, 1980). From May to July even juveniles may be found in the flooded lands in the vicinity of these lairs (Amestoy, 1982). When describing specimens of *A. pilimanus*, von Martens (1869) emphasized the coexistence of feminine and masculine gonopores. Thompson (1982) also studied the sex characters and ovarian histology in this species. She confirmed the observations of von Martens (1869), and at the same time noted that internally there exists a single gonad — ovary or testicle — from which two pairs of gonoducts emerge toward the gonopores located in the coxae of the third and fifth walking legs. Similarly to *P. varicosus* no testicular tissue was found in the female gonads. Unpublished observations of Rudolph, as well as anatomical and histological studies by Thompson (1982), support the existence of supernumerary gonopores in all the specimens of this species. They would also demonstrate that in this species there would be a "critical" size, under which it would not be possible to distinguish between the sexes externally. Over this size gonadic females would express this condition externally.

Parastacus saffordi *Faxon, 1898*

According to Faxon (1898), *P. saffordi* is a burrowing species. Buckup and Rossi (1980) found specimens of this species in shallow pits excavated by man around water upsurges. However, more recent records indicate the presence of the species in galleries burrowed in wet lands away from temporary or permanent water bodies. Its distribution comprises the eastern region of the state of Santa Catarina in Brazil and the outskirts of Montevideo, Uruguay (Hobbs, 1989).

Faxon (1898) also included *P. saffordi* among the *Parastacus* species, which typically present the coexistence of feminine and masculine gonopores in one same individual. Hay (1905) ratified this coexistence. To verify the probable existence of hermaphroditism in *Parastacus*, Turner (1935) studied the reproductive anatomy of 11 specimens of *P. saffordi*, and in none of them did he find a hermaphrodite gonad. In females he observed well developed oviducts and rudimentary spermiducts. In turn, in males he found well developed spermiducts and rudimentary oviducts.

Parastacus brasiliensis *(von Martens, 1869)*

This parastacid builds shallow non-ramified chambers on the margins of small lotic systems in the central region of the state of Rio Grande do Sul, Brazil. These dwellings serve as shelter for a single adult, while juveniles are found under leaves and vegetal detritus that accumulate in the low zones and still waters of these environments (Buckup and Rossi, 1980; Fries, 1984; Fontoura and Buckup, 1989).

When von Martens described this species (1869), he emphasized the presence of two pairs of gonopores in one same individual. Almeida and Buckup (1997) examined 46 *P. brasiliensis* specimens captured at Mariana Pimentel, Rio Grande do Sul (30°20′S; 51°22′W) and found that males and females presented an intersex genitalia, characterized by the presence of either one masculine or one feminine gonad with two pairs of gonoducts connected to gonopores located in the coxae of the third and fifth pair of pereiopods. Mature females had oviducts of a large diameter, connected to genital orifices unobstructed during the reproductive period and only partially obstructed during the period of reproductive inactivity, whereas the vasa deferentia were rudimentary and connected to slightly protruding phallic papillae. The males had rudimentary oviducts connected to fully obstructed female gonopores, while vasa deferentia had a very large medial region and were connected to male gonopores located in the apical end of a very protuberant phallic papilla. These authors, however,

did not find any gonad in a transitional phase. More recently, Almeida and Buckup (2000) have examined 92 specimens with sizes ranging between 11.7 and 40.0 mm SCL, captured in the same population aforementioned. They could verify in these specimens the existence of intersex males ($n=36$), transitional ($n=8$) and intersex females ($n=48$). Genitalia of intersex males and females showed the characteristics described by Almeida and Buckup (1997). In contrast, transitional specimens had fully obstructed female gonopores like those in intersex males and gonads with ovotestis characteristics whose ovarian components were in pre-vitellogenesis or primary vitellogenesis. The size of these individuals ranged between 27.1 and 35.5 mm SCL.

Parastacus defossus *Faxon, 1898*

This is a small, strongly burrowing species which builds complex and deep galleries in the low, marshy lands east and southeast of Rio Grande do Sul, Brazil, and in the outskirts of Montevideo and Laguna del Sauce, Uruguay (Buckup and Rossi, 1980; Amestoy, 1983). The whole life-cycle of this parastacid takes place inside these galleries, and according to the season of the year, specimens of different generations may be found living together in them (Amestoy, 1983).

When describing the species, Faxon (1898) emphasized the occurrence of masculine and feminine gonopores in the same individual, which was ratified by Hay (1905). Almeida and Buckup (1999) examined the sexual characters of 71 specimens with a SCL ranging between 12.4 and 29.9 mm, captured in the vicinity of Mariana Pimentel, Rio Grande do Sul (30°20′S; 51°33′W). The anatomic and histological analysis of their genitalia disclosed the existence of 33 intersex males and 37 intersex females. Such intersexuality is characterized by the presence in males and females of gonoducts and gonopores of the opposite sex. The oviducts of the females are wide and connect the ovary with feminine gonopores, either entirely or partially decalcified. The oviducts present in male specimens are very fine and connect the testicle to entirely calcified feminine gonopores. The females' vasa deferentia are thin and connect the ovary with phallic papillae, which are slightly protuberant. In contrast, vasa deferentia of the male specimens are cylindrical, of wide diameter in their mid-part and connect the testis to very protuberant phallic papillae. These authors could also verify that under 20.8 mm SCL all the specimens had gonopores with the same morphological characteristics as the males. However, the dissection disclosed that their gonads were already differentiated. In just one specimen with a SCL of 22.4 mm, it was found that the testicular and ovarian tissue coexisted in one same gonad. This individual presented entirely obstructed female gonopores, as in the male. The authors also verified that the abdomen of females had longer somites, higher pleurae and longer and wider uropodal branches compared to the male's abdomen, which would be related to an increment in abdominal volume for egg incubation.

Parastacus nicoleti *(Philippi, 1882)*

A strongly burrowing species which constructs galleries with multiple ramifications and large chambers at the level of underground water in marshy lands of the provinces of Osorno and Valdivia (39–41°S) in southern Chile (Kilian, 1959). *P. nicoleti* spends its whole life-cycle inside these galleries, apparently integrating family groups (Riek, 1972; Rudolph, 1997b).

None of the authors who analyzed the existence of supernumerary gonopores in *Parastacus* examined specimens of *P. nicoleti*. Notwithstanding, it was considered as a species similarly characterized by the coexistence of female and male gonopores in all its specimens. Rudolph (1990) analyzed for the first time the external sexual characters in 118 specimens from a single population. Of them, only 48.3% had both female and male gonopores, 42.3% had only female gonopores and the remaining 9.3% had one male gonopore besides the female ones. These observations were ratified by Rudolph (1995b); he described six gonopore patterns, which came to be the external expression of two basic sexual types, primary females — in prepuberty and puberty — and protandric hermaphrodites, the latter represented by a male phase, a transitional phase and two female phases. Protandric hermaphrodites in the male phase have ovotestis, with a small feminine anterior portion, small oocytes and rudimentary oviducts. In turn, the male region occupies a large part of the gonad and from it emerge well developed spermiducts, with an androgenic gland in its sub-terminal portion. In the transitional phase specimens, the feminine portion of the ovotestis occupies most of the gonad, with oocytes in vitellogenesis, highly developed oviducts and rudimentary spermiducts. In protandric hermaphrodites in the female phase, the only internal features of the masculine type are one or two very fine vasa deferentia (see Rudolph, 1995b). Permanent secondary sexual characters associated with egg incubation were also found in the

abdomens of primary pubescent females and in protandric hermaphrodites in the female phase.

Parastacus laevigatus *Buckup and Rossi, 1980*

The distribution of this species is restricted to the localities of Joinville and Cubatao Grande, northeast of the state of Santa Catarina, Brazil (Hobbs, 1989). Nothing is known about its biology. Buckup and Rossi (1980) described this species without mentioning its habitat or the presence or absence of supernumerary gonopores in the holotype and paratypes. However, Almeida and Buckup (1997) specified the criterion used to distinguish between sexes in the specimens analyzed by Buckup and Rossi (1980). This, together with observations of one of the authors (Almeida) on the external morphology of three individuals of this species, suggest that in *P. laevigatus* feminine and masculine gonopores might also coexist in the same individual.

Discussion

Of the 10 South American Parastacidae species, seven are strong burrowers, which inhabit underground waters in humid or marshy land and which apparently live in family groups. It is likely that *P. laevigatus* has the same behavior and occupies similar habitats. In turn, *S. spinifrons* and *P. brasiliensis* are slightly burrowing, live in individual lairs, with the former living in lentic and lotic waters and the latter only in lotic waters.

The current knowledge about external and internal sexual characters of South American Parastacidae is complete in certain species (*P. pugnax*, *P. nicoleti*, *P. varicosus* and *S. spinifrons*), scarce and fragmentary in others (*P. brasiliensis*, *P. pilimanus*, *P. saffordi*, *P. defossus* and *V. araucanius*) and nonexistent in one (*P. laevigatus*). Nonetheless, it is possible to visualize at least three sexual systems. The first is the gonochorism of *V. araucanius* and of the lake populations of *S. spinifrons*. The sparse data related to the former species suggest that all individuals have separate sexes. In the lake populations of *S. spinifrons*, the exclusive presence of males and females was confirmed (Rudolph, 1999b), with abdominal sexual dimorphism related to egg incubation (Rudolph, 1999a).

The second pattern is represented by the permanent intersexuality of the burrowing species *P. pugnax*, *P. varicosus*, *P. pilimanus*, *P. saffordi* and *P. defossus*. This intersexuality is externally expressed by the presence of masculine and feminine gonopores in all specimens and internally by the existence of a single gonad — either masculine or feminine — from which gonoducts of both sexes emerge. In these species, particularly in *P. pugnax* and *P. varicosus*, there is a "critical" size under which the morphology of masculine and feminine gonopores and of the abdomen is the same for all specimens. This does not allow externally distinguishing between sexes. However, anatomical dissections demonstrated that their gonads are already fully differentiated. With larger sizes than the "critical" size, the specimens may be externally recognized as males or females since the gonopores have changed in structure and, at the same time the females' abdomens have acquired a permanent reproductive morphology that allows incubation of eggs. Anatomical, morphological and histological data provided by different authors (von Martens, 1869; Faxon, 1898; Lönnberg, 1898; Hay, 1905; Turner, 1935; Thompson, 1982; Rudolph, 1997a; Rudolph et al., 1999; Almeida and Buckup, 1999) are consistent in many aspects and complementary in others. As a whole, they allow for discarding hermaphroditism of any kind in these species of *Parastacus*. Apparently this pattern challenges to a great extent the current knowledge about the control exerted by the androgenic gland on sex differentiation in Malacostraca. Their study could serve to prove the model that Sagi et al. (1997) and Khalaila et al. (1999) have suggested for the role of the androgenic gland in regulating the balance between maleness and femaleness in intersexual crayfish.

Concerning *P. brasiliensis*, the information compiled seems to be contradictory. Data provided by Almeida and Buckup (1997) clearly place the species in the pattern of permanent intersexuality exemplified by *P. pugnax*. However, Almeida and Buckup (2000) reported that the gonads of eight specimens (8.7% of 92 individuals examined) had ovotestis characteristics, so they were considered in a transitional state from male to female. We do not know of any previous study which contributed information in favor of one or the other options, except for the observations of external and internal sexual characters by von Ihéring (1892). But these were carried out in very few and poorly preserved specimens, so they do not help to clear up this contradiction. We believe that the description by Almeida and Buckup (2000) describes the true situation in *P. brasiliensis* that was not detected initially (Almeida and Buckup, 1997) due to small sample size (n=46).

The last pattern is the partial protandric hermaphroditism of *P. nicoleti* and of the fluvial populations

of *S. spinifrons*. In the former species the only *Parastacus* species in which not all individuals have supernumerary gonopores, six gonopore patterns have been described (Rudolph, 1995b). Two of them correspond to primary females — in prepuberty and puberty — with feminine gonopores only, and the remaining four to protandric hermaphrodites with supernumerary gonopores having a male phase, a transition phase and two female phases. In the fluvial populations of *S. spinifrons*, varying percentages (0–15.8%) of intersex specimens have been found. Anatomical and histological analyses of the genitalia in these intersex specimens allowed Rudolph (1999a, 1999b) to distinguish between intersex males, transitional phase individuals, and intersex females. All of them, however, had abdominal characteristics of males. Based on this evidence and considering the current knowledge on sex differentiation in Malacostraca (Charniaux-Cotton, 1975; Fingerman, 1987; Katakura, 1989; Hasegawa et al., 1993), we may postulate that these intersex specimens would represent transitional states in a change of sex, from male to female.

One species, *P. laevigatus*, cannot be assigned to any of the patterns mentioned above since it is not even certain whether all the specimens of this species have both masculine and feminine gonopores.

According to Hobbs (1974, 1988) and Scholtz (1995), the present Astacoidean taxa have evolved from a gonochoric ancestor with direct development which already inhabited fresh water. Could the variations of this ancestral gonochoric pattern observed in *Parastacus* species be adaptations to a burrowing life-style? Could there be some adaptive value in the intersexuality observed in the fluvial populations of *S. spinifrons*? Or, considering the conclusions of Carpenter (1978), is this an extreme example of developmental ability in the reproductive morphology and physiology of decapods? To answer these and other questions, further studies must be carried out on the sexual characters, as well as on the role of the androgenic gland in the regulation of sex differentiation. The social organization, sexual behavior, mating systems and physico-chemical aspects of the habitat of these species should also be studied.

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