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.

Acknowledgements

The authors thank Drs. Carlos Jara of the Universidad Austral de Chile and Amir Sagi of the Ben-Gurion University of the Negev for a critical reading of the manuscript. We gratefully acknowledge the financial support from the Dirección de Investigación y Postgrado of the Universidad de Los Lagos, Project 3020/97.

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