

INTERSEXUALITY AND ITS CONTROL BY THE ANDROGENIC GLAND IN THE CRAYFISH *CHERAX QUADRICARINATUS*

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Intersexuality

Intersex individuals, possessing both male and female characteristics, have been documented mainly in hermaphrodite species. Intersex characteristics may be limited to the external morphology or may extend to gonadal differentiation. Hermaphroditism—the condition of having both male and female functional reproductive organs in one individual—has been reported for a variety of crustaceans. Some cases of sequential hermaphroditism, in which intersex individuals serve as a transitional form during the process of sex change, have also been reported. Although sex changes occur only in a small percentage of crustacean species, protandry (change from male to female) predominates, representing approximately 82% of crustacean sequential hermaphroditic species (Brook *et al.*, 1994). Crayfish are generally regarded as gonochoristic, i.e., producing distinct male and female specimens. However, apparent intersexuality has been reported in several crayfish species (Farmer, 1972; Johnson and Otto, 1981; Chace and Moore, 1983). Most of the reports are based on the description of a single individual or a small number of specimens and comprise mainly a morphological and partial anatomical description; these reports thus do not facilitate an understanding of the functional sexuality of the specimens or indeed of the species. The two crayfish species in which intersexuality has

been adequately reported, the red claw crayfish *Cherax quadricarinatus* (Sagi *et al.*, 1996a), and the burrowing crayfish *Parastacus nicoleti* (Rodulph, 1995), present—nonfunctional hermaphroditism, including functional males with immature ovaries in *C. quadricarinatus* and partial protandric hermaphroditism in *P. nicoleti*.

Intersexuality in the red claw crayfish

The Australian red claw crayfish *C. quadricarinatus* (von Martens) is a gonochoristic species, attaining sexual maturity within 7 to 9 months (Rouse *et al.*, 1991) and developing a bilaterally symmetrical reproductive system. In males, this consists of pairs of testes, sperm ducts, androgenic glands and genital openings at the base of the fifth walking legs. Females have pairs of ovaries, oviducts and genital openings at the bases of the third walking legs. During the process of maturation in *C. quadricarinatus* females, changes occur in the morphology of the pleopods that facilitate their role in holding the newly deposited eggs (Sagi *et al.*, 1996b). The endopod of mature (vitellogenic) females is longer and wider than the exopod, and a mixture of plumose setae and long, thin simple setae are present on the endopod (Sagi *et al.*, 1996b). Intersex individuals with both male and female genital openings have been recorded in cultured *C. quadricarinatus* populations in a frequency of 1.2% to 17% (Brummett and Alon, 1994; Thorne and Fielder, 1991; Medley and Rouse,

1993; Sagi *et al.*, 1996a). Intersex individuals exhibit male secondary characteristics, such as the typical red patch on the claw, but do not have developed female secondary sexual characteristics, such as typical maternal setation. All *C. quadricarinatus* intersex individuals are functioning males, according to the presence of a male opening, a sperm duct, and a testis (containing viable sperm) on at least one side. An androgenic gland (AG) is attached to the subterminal region of each sperm duct (Sagi *et al.*, 1996a). When placed with receptive females, intersex individuals are able to mate and fertilize the eggs, producing viable progeny. However, not all visible female opening indicate the presence of a female reproductive system. Individuals, in which both male and female openings are present on one side, do not have an ovary on that side. An ovary with an oviduct is found only in those cases in which a female opening is present in the absence of a male opening on the same side. In intersex individuals that have both an ovary and a testis, the ovary exhibits a low gonadosomatic index (GSI); the value of this index is 0.12 ± 0.05 in intersex individuals compared with a value in mature females that may reach as high as 5. In this type of intersex individual, the diameter of the oocytes is small ($292 \pm 148 \mu\text{m}$ for the average intersex oocyte compared with over 1 mm for a mature ovary of a normal female), and the ovarian cytosolic polypeptide profile shows either a low concentration or no accumulation of yolk protein (vitellin). In all of the above-described features, the intersex ovary resembles that of the immature pre-vitellogenic female. Unlike true hermaphroditism, in which both male and female reproductive systems are functional, either simultaneously or sequentially, the intersex phenomenon in the red claw crayfish *C. quadricarinatus* represents a stable, rather than a transient state, since no changes were reported in intersex individuals monitored from 7 to 19 months of age (Sagi *et al.*, 1996a).

Regulatory role of the androgenic gland

Male differentiation and regulation of the genital apparatus and secondary sex characteristics in crustaceans are thought to be controlled exclusively by the AG hormone (AGH). In the absence of AGH, female differentiation occurs spontaneously (Charniaux-Cotton and Payen, 1988). The presence of AGH causes vitellogenesis inhibition (Berreur-Bonnenfant and Lawrence,

1984). This type of endocrine control has been demonstrated experimentally in Amphipoda and Isopoda, and in the decapod *Macrobrachium rosenbergii*, but it is probably true for all Malacostraca.

Effects of androgenic gland ablation in *C. quadricarinatus* intersex individuals

In four intersex individuals of *C. quadricarinatus*, all over one year old, AG ablation caused changes in the function of the reproductive system. After 60 days, the ovarian index of the female component (GSI) of the AG-ablated intersex individuals increased and reached a value of 4.7 ± 2.1 , which resembled the GSI value of vitellogenic females, as mentioned above. The oocytes also reached a mean diameter of $1.8 \pm 0.27 \text{ mm}$, which was similar to that of vitellogenic females. On the other hand, the reproductive index, which represent the weight of the male component of the reproductive system, decreased significantly to a value of 0.48 ± 0.15 , compared with normal value of 0.9 ± 0.13 . The external sexual characteristics, such as the width and situation of the endopod and the red patch on the propodus, remained male like, as they did in the control nonablated intersex individuals, see above.

These results show that the AG plays an important role in the regulation of intersex gonad activity. It appears to serve as the main agent that maintains the physiological situation in which the intersex testis is active while the ovary of the same intersex individual is arrested. In these respects, intersex *C. quadricarinatus* individuals present a unique model for the study of the various regulatory roles of androgenic and other hormones in sex differentiation and gonadal function in decapod crustaceans.

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