

Methyl farnesoate appears to be a crustacean reproductive hormone

H. LAUFER, A. SAGI, J.S.B. AHL* and E. HOMOLA

Department of Molecular and Cell Biology, The University of Connecticut, Storrs, CT 06268;

Marine Biological Laboratory, Woods Hole, MA 02543 (USA)

**College of Basic Studies, University of Hartford, West Hartford, CT 06117 (USA)*

Summary

Methyl farnesoate (MF) is an unepoxidated form of juvenile hormone III, which controls reproduction in insects and appears to serve the same function in Crustacea. MF is synthesized by the mandibular organs (MOs) and has been found in the hemolymph of both females and males in more than 25 species of crustaceans. MF is most actively synthesized by females during vitellogenesis. MF appears to be an active gonadotropin since implants of MOs into non-reproductives will increase gonad indices. In males, high titers of MF are associated with large reproductive systems and aggressive mating behavior.

Review

Several hormones that regulate reproduction in crustaceans include the gonad-inhibiting hormone (GIH), which may be the same as the vitellogenin-inhibiting hormone (VIH), gonad-stimulating hormone (GSH), and the androgenic gland hormones (AGHs). GIH/VIH and GSH have been described mainly in conjunction with female reproduction, whereas the AGHs are only associated with male reproduction. GIH/VIH is released from the sinus gland in the eyestalk and inhibits ovarian synthesis of yolk protein, vitellogenin, *in vitro* (Eastman-Reks and Fingerman, 1984; Quackenbush and Keeley, 1987).

GSH is reported from the thoracic ganglion (Eastman-Reks and Fingerman, 1984) and the brain (Anilkumar and Adiyodi, 1980; Gomez, 1965; Hinsch and Bennett, 1979; Takayanagi et al., 1986) and stimulates ovarian growth and maturation. The AGHs are produced by androgenic glands and control sexual differentiation (Charnaiux-Cotton, 1954). In this paper we discuss methyl farnesoate (MF), which is found in both sexes, and may be a reproductive hormone common to many species of crustaceans.

MF is an unepoxidated form of juvenile hormone III, which in immature stages of insects controls larval development and in adults controls reproduction. MF is synthesized by the mandibular organs

(MO) Laufer et al., 1986, 1987a, 1987b) as revealed in cultured glands by radiochemical labelling, and was first detected in the hemolymph of the spider crab, *Libinia emarginata*, using gas chromatography/mass spectrometry (Laufer et al., 1987b). Since then, it has been identified in the hemolymph of both males and females and in over 25 species of Crustacea (Landau et al., 1989; Laufer and Borst, 1988; Sagi et al., 1991; Tobe et al., 1989).

Although the role of MF in reproduction is not entirely clear, it appears to be related to gonadal growth and possibly also to maturation in both sexes. MF may act as a gonadotropin since implants of active MOs stimulate enlargement of the ovary in immature female *L. emarginata* (Hinsch, 1980). MO activity is associated with development of the ovary in that it is lowest in juvenile and pre-vitellogenic females and greatest during vitellogenesis, as demonstrated *in vitro* with isolated MOs (Laufer et al., 1986). MF induces small but significant increases in hemolymph levels of vitellogenin when injected into eyestalkless adult female *L. emarginata* (Vogel and Borst, 1989).

In males, reproduction is even more complex because there are several morphotypes, all of which have sperm in their reproductive tracts, and they display different mating behaviors. Although there are a number of species that have behaviorally distinct male morphotypes such as the amphipod *Jassa falcata* (Borokowsky, 1985), the freshwater prawn *Macrobrachium rosenbergii* (Ra'anan and Sagi, 1985), the isopod *Paracereis sculpta* (Shuster, 1987), and the Snow and Tanner crabs (Conan and Comeau, 1986; Donaldson and Adams, 1989), investigations into the endocrinology of these types has so far only been done in the spider crab *L. emarginata*.

The male morphotypes of *L. emarginata* are distinguished by claw length relative to carapace length and the condition of the exoskeleton (Homola et al., 1991). There are large- and small-clawed males that appear velvety due to the pubescent nature of the epicuticle covering the exoskeleton and are referred to as unabraded. These males have recently molted within the past season. They have low MF titers in their hemolymph, relatively inactive MOs, and small reproductive systems. The other morphotypes, which include both large- and small-clawed forms, lack the pubescence because the epicuticle has been worn away, and these are therefore called abraded. These crabs have not molted for about a year or more. Compared to the unabraded males, the abraded crabs have

MF titers that are 2–3 fold higher, their MOs are 2–6 times more active, and their reproductive systems are 3–4 times larger.

These morphotypes are just as distinct behaviorally. Large-claw abraded males actively compete for, mate with, then carry and guard receptive females (Laufer et al., 1992; Sagi et al., 1992). Small-claw abraded males utilize a non-competitive "sneak-mating" tactic. That is, they either mate in isolate or quickly copulate when the large-claw abraded males are "distracted," but they do not carry or guard the females after mating. The unabraded males do not display any mating behavior. Thus, the large-claw abraded males are the primary reproductives (Homola et al., 1991).

In insects, high levels of juvenile hormone (JH) are necessary for the development and maturation of the reproductive system and for the display of mating behavior (see Downer and Laufer, 1983). The lack of mating behavior, especially in adults, is attributed to low levels or the absence of JH, and in some species gonadal regression (DeWilde, 1983). This condition is referred to as reproductive diapause and commonly occurs after the molt to the adult form (Denlinger, 1985) and between breeding seasons. It appears then that the lack of mating behavior, low levels of MF in the hemolymph, and the small reproductive system exhibited by unabraded male *L. emarginata* suggests that these crabs are in a state of reproductive diapause.

The synthesis of MF by the MOs and its high titer in the hemolymph of vitellogenic females and the reproductively active male morphotypes are strong evidence that MF is indeed important for reproduction in crustaceans.

Acknowledgements

We would like to thank David Dodge and the staff of the New England Utilities Environmental Laboratory at Millstone Power Plant for the collection of *Libinia emarginata*, and Dr. Larry Renfro for help with their transportation; the technical advice of Dr. F. Mauri of the University of Connecticut Biotechnology Center; and for the use of the HPLC facilities. This work was supported in part from the Sea Grant College Program to H.L.; a Fulbright Scholarship, and a Binational Agricultural Research Development Foundation fellowship to A.S.

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