

REPRODUCTIVE PATTERNS IN MURICIDAE (PROSOBRANCHIA : NEOGASTROPODA)

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ABSTRACT

The ontogeny from the time of deposition of eggs in capsules until the larvae metamorphose and become juveniles, is reviewed for muricid gastropods. The model used for the modes of development, can be applied to families, genera and perhaps to species. Conspecific variation in the mode of development is known as poecilogony. Variation in mode of development in geographically separated populations of three species of the genus *Chicoreus*, indicates either poecilogony or the existence of more than one species. However, the critical review of poecilogony by Hoagland & Robertson (1988) shows, that it is difficult to prove which alternative is the correct one.

In at least two species of the genus *Chicoreus* and one species of *Ocenebra* most females possess a penis. The function of the penis is still open to debate. It is speculated that these species are either protandric hermaphrodites or just possessing secondary sexual characters.

INTRODUCTION

During previous work describing the morphology of egg capsules, larvae, adult shells and soft parts of three species of *Chicoreus* (Middelfart 1992, 1993a-c), several questions arose which needed discussion.

Firstly, reviews of the diversity of developmental patterns exist for the prosobranchs (Mileikovsky, 1971; Shuto, 1974; Thorson, 1946), whereas specific evaluations of the actual developmental paths in the muricids is lacking. In this paper an overview of patterns of development of muricids is given together with definitions of the terms lecithotrophic, planktotrophic and "nurse egg" - feeding. It should be noted that the composition of developmental paths given in this paper does not equal the general composition given in Mileikovsky (1971), Thorson (1946) or Shuto (1974). Furthermore, the definitions of developmental modes are fitted to the present knowledge of muricid reproduction.

Secondly, Middelfart (1992) described the mode of development in *Chicoreus torrefactus* (Sowerby, 1841) and *Chicoreus brunneus* (Link, 1807). The modes described do not match the descriptions given by Risbec (1932) for *C. brunneus*, and Cernohorsky

(1966) for *C. torrefactus* from the Pacific Ocean. Geographical variation in the mode of development of *Chicoreus ramosus* (L., 1758) is revealed in this paper, where the description from Thailand differs from descriptions from the Red Sea (ref. see later). These cases of variation in allopatric populations point in the direction of poecilogony, defined as: "...the presence of more than one distinctive kind of development in the same sexually reproducing species, i.e., a polymorphism in development..." (Hoagland & Robertson, 1988). But, as Hoagland & Robertson (1988) pointed out, poecilogony is a very rare phenomenon and very difficult to prove. Thus, this paper emphasises the discussion of the possibilities of testing whether we are dealing with poecilogony or species complexes in the three *Chicoreus* species.

Thirdly, Middelfart (1993a & 1993c) showed that the sex characters of female *C. ramosus* and *C. brunneus*, in most cases include a penis. This phenomenon has only previously been reported for *Ocenebra erinacea* (L., 1758) from Arcachon, France, by Feral (1973). Here I evaluate the actual knowledge of this sexual phenomenon in muricids.

RESULTS AND DISCUSSION

Mode of development

Figure 1 may illustrate the plasticity in intracapsular development, extracapsular paths which have been demonstrated, and paths which can be suspected to occur.

The model was originally made to visualise developmental patterns for the Muricidae, but is also representative for the taxa *Thais* and *Chicoreus* which have some intrageneric diversification.

The model illustrates three main paths which I believe to exist in the muricid family:

- The veliger larva is lecithotrophic for a variable (usually short) period inside the egg capsule, hatches in a more or less developed veliger stage without sufficient stored nutrition for further development and metamorphosis and, therefore, has to feed on phytoplankton. That is the planktotrophic mode.
- The veliger larva is lecithotrophic for a long period inside the egg capsule, and hatches just before metamorphosis ("veliconcha") or later, as a juvenile. This is the "true" lecithotrophic larva.
- The veliger larva feeds on "nurse" eggs during the veliger stage inside the egg capsule and hatches as a juvenile.

It is uncertain whether species which feed on intracapsular "nurse" eggs may have a planktotrophic stage. *Thais haemastoma* (L., 1758) has been recorded to have pelagic development in Florida, but non-pelagic development in the West-Indies and "nurse" eggs (e.g. Burkenroad (1931), and Lamy (1928); both in Thorson, 1946). But, as Barkati & Ahmed (1983) write "we wish to point out here that some workers feel that the above reference to direct development in the West-Indian species of *Thais* is based on misinformation (= misidentification?)", it can hardly be used as proof for that pathway.

Poecilogony in *Chicoreus*

Figure 1 illustrates the essence of poecilogony through the possible mutual connections between A, B and C, because the figure emphasises that a

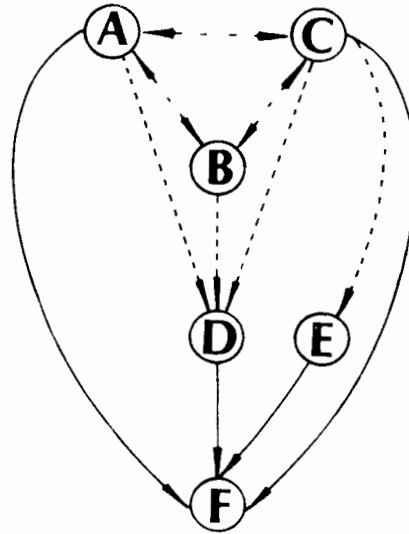


Figure 1. Embryo - larvae - juvenile continuum. — verified path, --- questionable path, - - - questionable intraspecific plasticity. **A:** much yolk, **B:** little yolk, **C:** "nurse eggs", **D:** planktotrophic larvae, **E:** lecithotrophic larvae and **F:** young snail/juvenile. **A - F:** *Ocenebra erinacea* (Fretter, 1941), *Urosalpinx cinerea* (Webber, 1977); **A or B - D - F:** *Pterynotus erythostomus* (Radwin & D'Attilio, 1976); **D - F:** *Chicoreus brunneus* (Middelfart, 1992), *C. ramosus* (Bussarawit & Ruangchua, 1991), *C. torrefactus* (Middelfart, 1992); **C - E - F:** *Chicoreus ramosus* (Hoagland & Robertson, 1988 (misidentification? = *Chicoreus virginicus* Röding, 1798 (*C. virginicus* mistakenly identified as *Murex incarnatus* (D'Asaro, 1991) which is syn. for *C. ramosus* (?Vokes, 1971, Houart, 1992))); **C - D:** *Thais haemastoma* (Thorson, 1950 (in Radwin & D'Attilio, 1976; Barkati & Ahmed, 1983; Lyons & Spight, 1973)); **C - F:** *Nucella lapillus* (Fretter & Graham, 1962), *Thais emarginata* (LeBeouf, 1971), *Chicoreus torrefactus* (Cernohorsky, 1966), *Thais haemastoma* (Thorson, 1950 (in Radwin & D'Attilio, 1976; Barkati 1983; Lyons & Spight, 1973)).

change in embryonic development most likely results in a change of the succeeding developmental path, considering the three previous mentioned main paths.

But, poecilogony has actually not been proven yet for any neogastropod and especially not for the muricids (Hoagland & Robertson, 1988). The cases which have been postulated are questionable because misidentification has been suspected (Hoagland & Robertson, 1988) or because descriptions are too weak for conspecific comparisons (Middelfart, 1993d).

Confusion in developmental mode of C. ramosus

The mode of development of *C. ramosus* has been described from the Andaman Sea, Thailand, by Bussarawit & Ruanghua (1991), Middelfart (1992) and Steinfeldt (1992). Here, the embryos feed on albumen and hatch in an early veliger stage. The pelagic development may be around two weeks (13 - 15 days; Steinfeldt, 1992), but the sinusigera character, on the outer shell edge, can be found in some individuals already after 5 days (Middelfart, 1992), an indication of readiness for settling. In the Gulf of Mannar, India, Ramesh *et al.* (1992) showed that the first larvae of *C. ramosus* metamorphosed after 45 days in the plankton.

Spight (1977) and D'Asaro (1991) respectively states that *C. ramosus* from the Red Sea has veliconcha stage (equals short lecithotrophic larval stage) and 3 days pelagic larval stage. Both authors refer to Gohar & Eisawy (1967) and refrain from stating anything about intracapsular nutrition (note that I am not in the possession of Gohar & Eisawy's paper). On the other hand, Hoagland & Robertson (1988) state that *Murex incarnatus* (Röding) (a synonym of *C. ramosus* in Houart (1992) but questionable synonym in Vokes (1971)), from the Red Sea, has "nurse eggs" and a transition between direct development and veliconcha stage, where most larvae hatch one day and metamorphose the day after, while the rest crawl directly out of the egg capsule the second day after rupture of the escape aperture (note that Hoagland & Robertson also refer to Gohar & Eisawy (1967)). Apparently Hoagland & Robertson's reference (Gohar & Eisawy 1967) uses *M. incarnatus* for the wrong species, as D'Asaro (1991, p.18) states that *M. incarnatus* from Gohar & Eisawy's research has been identified as *Chicoreus virginus* (Röding 1798) by Soliman in 1987.

Thus, based on the knowledge from the Red Sea, India and Thailand it can be stated that *C. ramosus* may have from 3 to 45 days of pelagic development. This variation might then be an incipient state of poecilogony or an intraspecific plasticity controlled by local environmental condition.

Variation in developmental modes in C. torrefactus and C. brunneus

C. torrefactus and *C. brunneus* both show polymorphism in the mode of development (compare Cernohorsky (1966) with Middelfart (1992) for *C. torrefactus*, and compare Risbec (1932) with Middelfart (1992) for *C. brunneus*). *C. torrefactus* from Fiji Archipelago and *C. brunneus* from New Caledonia both have direct development. *C. torrefactus* has "nurse" eggs and *C. brunneus* has questionable intracapsular nutrition (Cernohorsky, 1966; Risbec, 1932). This does not match the findings from Phuket, Thailand, where the two *Chicoreus* species have two to three weeks planktotrophic development (Bussarawit & Ruanghua, 1991; Middelfart, 1992).

This discrepancy may be explained in various ways.

(1) Poecilogony due to genetic variation in a widely distributed species, which can be referred to as incipient speciation. Egg capsule morphology differs geographically for both species (compare Middelfart (1992) with D'Asaro (1991) and Cernohorsky (1966) for *C. brunneus*, compare Middelfart (1992) with Risbec (1932), and D'Asaro (1991) for *C. torrefactus*).

According to Hoagland & Robertson (1988) the following conditions have to be satisfied: Poecilogony exist in a species:

A if genetic (allozyme) data for sympatric individuals demonstrates that interbreeding occurs between individuals with different larval types, or if the individuals are fixed for alternate alleles and hence are not interbreeding.

B if a single individual observed in the laboratory produces two types of larvae, *i. e.*, under varying environmental or nutritional conditions.

C if cross-breeding data for allopatric populations, combined with allozyme or other molecular genetic studies, show that (a) cross-fertilisation occurred, (b) viable offspring were produced, (c) the offspring in turn are capable of breeding and reproducing with each other and

the parental types, and (d) the cross-breeding event could plausibly occur in nature as well as in the laboratory. The heritability and genetics of mode of larval development need to be established.

The two *Chicoreus* species treated here fall in the (C) category. Thus, the biological species concept should be proven between the allopatric populations. This will however be a very difficult task, since there are big problems in doing so on the large geographical scale the phenomena falls in. Since this cannot be achieved on a reasonable time scale, future work with widely distributed species, as the *Chicoreus* species, should be restricted to thorough descriptions of adult spawners and their reproductive products.

(2) The descriptions of early life stages of *C. brunneus* and *C. torrefactus* from the Pacific might stem from sibling species. Houart (1992) mentions that *C. torrefactus*, *C. brunneus*, *Chicoreus microphyllus* (Lamarck, 1822) and *Chicoreus banksii* (Sowerby, 1841) probably have the most variable shells in the genus *Chicoreus*. Houart (1992) suspects this to be caused by the wide distribution areas and thereby variable ecological conditions which often affects the shell morphology (Kincaid, 1957). In this case, however, the mode of development, and egg capsule morphology vary, as well. Thus, the existence of sibling species could be suspected in these *Chicoreus* species.

(3) Misidentification is also a possibility. Risbec (1932), did not write how he obtained the egg capsules of *C. brunneus*. It is unknown if he actually observed spawning *C. brunneus* in the laboratory or in the sea. Hence, it cannot be excluded that these egg capsules came from another species.

Sex differentiation in *Chicoreus*

Muricid gastropods do not have significant sexual dimorphism in the shells, and the soft parts therefore have to be emphasized in sex determination. It is, however, not sufficient to register if a penis is

present or not. Initially, the sex of *C. ramosus* from the Andaman Sea was determined by looking for the penis, even though the presence of some individuals with a rather small penis were observed and very few females were found during 1991 (Thapnu pers. comm.). The morphological and anatomical work of Middelfart (1993a & 1993c) revealed that presence of penis is in fact not sufficient for sex determination, the reproductive system has to be viewed as a whole in order to accurately determine sex. The main part of *C. brunneus* females and a still unknown percentage of *C. ramosus* and *C. torrefactus* females possess a penis. Thus, only if the shell of the *Chicoreus* specimen is crushed, leaving the entire reproductive system to be seen through the integument, can an appropriate sex determination be made (Middelfart, 1993a & 1993c).

Feral (1973) found that females of *Ocenebra erinacea* (L., 1758) from Arcachon, France, possessed a penis like *C. brunneus*, *C. ramosus* (Middelfart, 1993a&c) and *C. torrefactus* (Middelfart, unpublished). Feral concluded that:

- There was no displacement in sex ratio over the entire size range of the species.
- There was no evidence of sexual change in the histological examination of the gonad.

Thus, Feral suggested gonochorism and rejected any form of hermaphroditism in *O. erinacea*.

The sex ratio related to size is hardly convincing, as small individuals (<20 mm) are rarely found. What is the size at maturity in *O. erinacea*? If it is under e.g. 20 mm (which is likely, as Feral noted one 10 - 12 mm female, with a penis, in May), then the conclusion would be erroneous. Sex change might take place at, or before, the first breeding. Thus, the species would be a protandric hermaphrodite. But if the displacement in frequency distribution was lacking, in the whole range from maturity to maximum attainable size, then Feral's conclusion would be convincing.

A further indication of sex change in *O. erinacea* was described by Fretter (1941) who mentioned a

remnant of the gonopericardial duct: "Close to its opening (vesicula seminalis) into the prostate the vas deferens gives off a short diverticulum towards the pericardium, and the blind end of the diverticulum is connected with a slight prominence on the pericardial wall by a band of dense connective tissue and muscle fibres.... In *Calyptrea sinensis* (Giese, 1915) animals changing from male to female develop a gonopericardial duct, and this first appears as a strand of dense mesenchyme bridging the gap between the vas deferens and the pericardium. It therefore appears that in the male of *Ocenebra erinacea* this is the remnant of a gonopericardial duct."

I believe the "predisposition for" instead of "remnant of" a gonopericardial duct, could be used if Ferals research is considered.

CONCLUSION

A considerable amount of literature on early stages of muricid gastropods exists today. Unfortunately for the study of diversification in developmental patterns, many of these papers do not present the whole developmental mode from the intracapsular feeding type to metamorphosis of the veliger. Some developmental modes are therefore difficult to es-

tablish and might not even take place in the muricids, yet others might exist which we are not aware of. The early life stages of muricid gastropods is a major key to our understanding of this family in the sense of phylogeny, cladistics, zoogeography, taxonomy and for that matter ecology.

The variation in developmental patterns of the three *Chicoreus* species discussed in this paper is thus a flag to alert us, that more systematic research, such as genetical analysis and interbreeding sessions, has to be performed on these species in order to reach a better understanding of whether we are dealing with species complexes, misidentifications or poecilogony. Generally, it would be helpful in future comparisons if spawning adults were described along with the characters of the reproductive products. This procedure would prevent or at least reduce problems with the identity of the species in question.

The way in which the process of sexual differentiation occurs in the genera *Ocenebra* and *Chicoreus* has to be established. One essential point is that all of the neogastropods are believed to be unisexual (dioecious, gonochoristic), thus, suggesting evolutionary convergence in the ability to change sex in all three orders of prosobranchs.

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