

Independent evolution of reproductive modes in viviparous freshwater Cerithioidea (Gastropoda, Sorbeoconcha) - a brief review

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“To Dr Hans Kuiper, sphaeriid expert, who started his diplomatic career in Berlin.”

In molluscs the majority of marine species is oviparous, whereas viviparity is frequently found among freshwater inhabitants. Here some findings from limnic gastropods are discussed and their evolutionary implications outlined. Recent studies reveal that live-bearing strategies have not only evolved repeatedly and independently among limnic gastropods, but also within limnic Cerithioidea, a diverse and speciose caenogastropod superfamily. Some of its constituent taxa evolved breeding along separate evolutionary avenues, involving distinct morphological structures (uterine brood sacs vs. subhaemocoelic brood pouches) and life-history strategies including nourishment of the brood via matrotrophy, as found in some species of Thiaridae s.str. It is concluded that (i) a uterine viviparous strategy, as found in lacustrine taxa from Lake Tanganyika (*Lavigeria*, *Tiphobia*), Lake Biwa in Japan (*Semisulcospira*) and from the central lakes on the Indonesian island of Sulawesi (*Tylomelania*), evolved several times in parallel, and (ii) that the subhaemocoelic brood pouch also derived convergently at least in the marine Planaxidae, some SE Asian Pachychilidae and the Thiaridae s.str., while the mesopodial brood pouch of the Tanganyikan paludomid *Tanganyicia rufofilosa* has to be considered again an independently evolved structure.

Key words: viviparity, limnic gastropods, brood pouch, matrotrophy, life-history.

INTRODUCTION

While in molluscs the overwhelming majority of marine species remained oviparous, viviparity represents a feature that is predominantly found in freshwater inhabitants. Live-bearing is characteristic among gastropods such as the Viviparidae (*Viviparus*, *Bellamyia*, *Notopala*), some limnic species of the Hydrobiidae [e.g. *Potamopyrgus antipodarum* (Gray, 1843)] and the pantropical Thiaridae sensu lato, as well as among bivalves such as Sphaeriidae, some species of Corbiculidae and Mutelidae; for a review and references see e.g. Glaubrecht (1996: 85-91). In addition, we recently found evidence for a novel brooding mode also among the freshwater limpet snail *Protancylus*, a basommatophoran endemic to Sulawesi, representing the first known case among limnic pulmonates (Albrecht & Glaubrecht, in press).

Retaining eggs and even more advanced juveniles in a specific incubatory structure, i.e. giving birth to living young, was first reported for freshwater gastropods by the French malacologist Louis Raymond (1852) for the thiarid *Melanoides tuberculata* (M uller, 1774). He described animals from Algeria in North Africa, erroneously assuming, though, that the newly hatched juveniles return at night into a marsupial-like pouch situated in the neck region of the female (see details in Glaubrecht, 1996: 117-124). Nevertheless, Raymond (1852: 329) anticipated the importance of this structure for comparative anatomy of so-called „melaniids“, and he correctly distinguished this extra-uterine brood pouch from those anatomical structures involved in Viviparidae. As it is evident from a note in Von Martens (1897: 29), who also reported this peculiar reproductive mode in

"*Melania*" *lateritia* (a synonym for *Tarebia granifera*) and some other closely related species from northern Sulawesi in Indonesia, it was long assumed that all "melaniids" possess such a brood pouch and, therefore, are all viviparous.

Given the striking association of brooding gastropods with their occurrence in fresh water prompted many speculations on correlation and causation, especially in the superfamily Cerithioidea, a group where freshwater taxa account for the vast majority of viviparous species. In this context, viviparity has been discussed (i) not only in connection with but as important innovation for the colonization of fresh water in general (e.g. Calow, 1978), and (ii) the radiation and rapid speciation within certain groups, in particular the "thalassoid" (i.e. marine-like) gastropods of Lake Tanganyika (Boss 1978; Michel, 1994); for a discussion see Glaubrecht (1996, 1999).

Two factors, however, have long hampered a thorough evaluation of the evolutionary implications of viviparity in molluscs. First, since taxonomic confusion and lack of phylogenetic knowledge often existed in case of the highly variable limnic malacofauna, a clear differentiation based on systematics and phylogeny of these taxa in question and of the morphological structures involved in incubation was essentially missing.

Second, the evolutionary implications of viviparity have been interpreted in contradictory ways. For example, viviparity in gastropods was discussed as either being correlated with a widespread distribution of brooding taxa, as e.g. in the pantropical thiarid *Melanoides tuberculata* or the pachychilid *Brotia costula* (Rafinesque, 1833) in Southeast Asia (e.g. Davis, 1982: 391), or as an causal explanation for the speciation and lacking dispersal ability in *Lavigera* from Lake Tanganyika as opposed, for example, to oviparous *Spekia zonata* (Woodward 1859) (see e.g. Cohen & Johnston, 1987; Michel, 1994); for a detailed discussion and refutation of these erroneous hypotheses see Glaubrecht (1996, 1999), Strong & Glaubrecht (2002) and Köhler et al. (2004).

This situation has improved over the past couple of years for limnic cerithioidean gastropods as we are striving for a better understanding of the systematics of this group using cladistic analyses combining morphological studies with molecular data (Glaubrecht, 1996, 1999, 2000; Lydeard et al., 2002; Wilson et al., 2004; Glaubrecht et al., unpubl. data). Therefore, based on a sound phylogenetic framework of the formerly so-called "melaniids" and detailed studies of the morphological structures involved in the viviparity of individual taxa, it is possible now to evaluate the degree of convergence in their reproductive modes.

DISTINCT ANATOMICAL MODIFICATIONS

It is most commonly found among viviparous gastropods that they modified their pallial oviduct into a brood chamber or sac (i.e. an "uterus"), where eggs and embryos are retained until shelled juveniles hatch. This kind of internalized brood care in a uterine gonoduct is realised, next to the marine *Littorina saxatilis* (Olivi, 1792) and *Littoraria angulifera* (Lamarck, 1822) (Littorinidae), for example, in limnic *Viviparus*, *Bellamyia* and *Notopala* (Viviparidae) as well as in *Potamopyrgus antipodarum* (Hydrobiidae). In the past it was occasionally assumed that a uterine brood pouch is also found in Thiaridae s.str. (see e.g. Pilsbry & Bequaert, 1927: 300, for *Melanoides tuberculata*). However, this is erroneous and was not founded in anatomical studies as will be described below, since we find a completely distinct anatomical structure in the brooding "thiarids", as it was already noted in Raymond (1852).

Actually, among Cerithioidean gastropods viviparity via uterine gonoducts is known only in (i) the family Paludomidae, and here exclusively in members of the Tanganyikan fauna (*Lavigeria*, *Potadomoides* and *Tiphobia*), (ii) the Asian pleurocerid *Semisulcospira* and (iii) the two Australasian pachychilid genera *Tylomelania* and *Pseudopotamis*, endemic to Sulawesi and two Torres Strait Islands, respectively (see survey in Glaubrecht, 1996; also

Glaubrecht & Von Rintelen, 2003; Von Rintelen & Glaubrecht, 1999, 2005). The pleurocerid and pachychilid brooders have modified their morphologically open pallial gonoduct (as it is typical for Cerithioidea) into a *functionally* closed tube, while it is a morphologically closed tube - through the fusion of medial and lateral lamina - in the Tanganyikan paludomids (Glaubrecht, 1996; Glaubrecht & Strong, unpubl. data). It remains to be studied whether a closed gonoduct, as e.g. in the Asian pleurocerid *Semisulcospira*, has to be considered as consequence or cause of retaining eggs in the uterus. However, intra-uterine feeding has not been demonstrated so far in any of the above mentioned taxa. Thus, in all cases the embryos rely on egg yolk or albumen for nourishment.

BROOD POUCHES IN "MELANIID" GASTROPODS

In contrast, a unique anatomical structure can be found among some, but not all, limnic Cerithioidea, most notable in the family Thiaridae *sensu stricto*, but also in some Southeast Asian Pachychilidae. These limnic gastropods were long treated in the literature as "Melaniidae", but this has to be corrected for both nomenclatorial and taxonomical reasons (see details in Glaubrecht, 1996, 1999). Since cladistic analyses revealed several independent lineages among limnic Cerithioidea, both using molecular genetics (Lydeard et al. 2002) and morphological data (Glaubrecht, 1996, 1999; Glaubrecht et al., unpubl. data), we here need to differentiate and discuss separately the two clades exhibiting this special incubatory structure.

Thiaridae *sensu stricto*

True thiarids, or Thiaridae *sensu stricto*, inhabit fresh water and brackish water both in lotic (including springs, creeks, rivers and streams) and lentic habitats (lakes and ponds) mostly in tropical to subtropical regions worldwide. Instead of laying eggs they exclusively brood their young in a so-called subhaemocoelic brood pouch, thus an extra-uterine structure. This unique incubatory chamber is situated in the right head-foot (propodium) and extends posteriorly into the neck region of the female. It is compartmentalized and was found in some thiarids to exhibit nutritive tissue allowing "pseudoplacental" nourishment of the young (see below).

It was hypothesized that this pouch evolved through the process of invagination of the genital groove and ovipositor organ which is commonly found in other oviparous Cerithioidea, but is lacking in all viviparous thiarids. Thus, the inner lining of the brood pouch, which is ciliated and/or secretory, is of ectodermal origin in Planaxidae as well as Thiaridae *s.str.* (see Houbbrick, 1987; Glaubrecht, 1996).

This subhaemocoelic brood pouch has to be considered a synapomorphy of all viviparous Thiaridae *sensu stricto*. However, since a similar structure is found in at least one other limnic Cerithioidean family, viz. some - but not all - Pachychilidae (as it is discussed below), and in marine Planaxidae (Houbbrick, 1987), it has evolved three times convergently. In addition, it should be mentioned that another uniquely derived internal (subhaemocoelic) brood pouch is found in *Tanganyicia rufofilosa* (Smith 1880), a thalassoid paludomid from Lake Tanganyika. However, in this case the pouch is situated in the mesopodium (see Strong & Glaubrecht, 2002), which underscores the conclusion drawn here of a convergent evolution of these incubatory structures in Cerithioidea. Since no indication for nourishment via matrotrophic epithelium in the brood pouch was found in the latter monotypic genus, its reproductive mode is ovoviviparous; for a review of ovoviviparity in gastropods, see Glaubrecht (1996: 85-91) and the discussion below.

Pachychilidae

While pachychilids in the Neotropics (e.g. *Pachychilus* and *Doryssa*) and the Ethiopial region (*Potadoma* in African and the Madagassy *Melanatria*) are oviparous, only those in

Southeast Asia and Australia are viviparous. An exceptional ovoviviparous (or viviparous lecithotrophic) strategy was recently found in the two known species of the endemic Philippine pachychilid *Jagara*, that exhibit brood care with eggs and embryos retained within the mantle cavity (see details in Köhler & Glaubrecht, 2003).

In contrast, a truly subhaemocoelic brood pouch is found in three other pachychilid genera from Southeast Asia, viz. *Paracrostoma*, *Brotia* and *Adamietta*; for an outline of the new systematization based on cladistic analyses of Pachychilidae and detailed descriptions and biogeography see Köhler & Glaubrecht (2001, 2002, 2003, submitted) and Köhler et al. (2004).

However, even in these pachychilids the reproductive mode is ovoviviparous (or viviparous lecithotrophic), since no indication was found for nourishment via a truly matrotrophic epithelium in the brood pouch, as is described briefly for the viviparous matrotrophic Thiaridae sensu stricto in the following.

DISTINCT LIFE-HISTORY STRATEGIES

Within the Thiaridae sensu stricto we find two distinct viviparous modes that are correlated with the amount of nourishment provided by the female (Glaubrecht, 1996, 1999, and unpubl. data; Schütt & Glaubrecht, 1999). In contrast, only one of these two distinct life-history modes is known so far from SE Asian Pachychilidae.

In some genera and species of true Thiaridae, e.g. *Balanocochlis*, *Thiara amarula* (Linné, 1758) and *Stenomelania aspirans* Hinds, 1844, eggs within the subhaemocoelic brood pouch develop only into the veliger stage before they are released into the water in great numbers. Since the developing embryos or veligers are not nourished within the female's pouch, there is no supply of nutrients other than those enclosed within the egg capsule. This lack of provision via nourishing tissue is distinguished here as viviparous lecithotrophic mode.

In contrast, in other thiarid species (as well as brooding pachychilids) the embryos develop within the pouch up to the stage of shelled juveniles. Their shells often comprise up to 5 or 7 whorls when hatching, as e.g. in *Melanoides tuberculata*, *Thiara scabra* (Müller, 1774) or *Tarebia granifera* (Lamarck, 1822). In these thiarids the juveniles are nourished, supplementing the yolk provided with the egg, by matrotrophy, i.e. by nutrients secreted from a placenta-like epithelium lining the inside of the subhaemocoelic brood pouch. This unique brood pouch structure involving a secretory tissue has been named a "pseudoplacenta", and is considered a special adaptation of some (but not all) Thiaridae sensu stricto (see Glaubrecht, 1996, 1999). While the former strategy involving the release of veligers should be distinguished as ovo-viviparous mode, matrotrophy via pseudoplacenta is to be regarded as eu-viviparous (or viviparous matrotrophic) mode.

Interestingly, while the former reproductive mode - viz. incubation of embryos up to the veliger stage only - is common among brooding marine Planaxidae, those SE Asian Pachychilidae with subhaemocoelic brood pouch and uterine brood chambers both exhibit the second mode, i.e. incubation of shelled juveniles. However, they not only lack a free veliger stages, but also any epithelial nutritive tissue involved in a truly eu-viviparous mode as found in Thiaridae. In contrast to the latter, these SE Asian viviparous lecithotrophic pachychilids were not found yet to nourish their brood via matrotrophy, but they apparently invented several other ways of nursing their young; for more details see Köhler & Glaubrecht (2001, 2003), Glaubrecht & Von Rintelen (2003), Köhler et al. (2004) and Von Rintelen & Glaubrecht (2005).

In addition, according to our studies we distinguish in both limnic families discussed here the so-called "r-strategy", as e.g. in *Thiara amarula* and *Stenomelania aspirans* among the true Thiaridae, which is comparable in terms of the numerous juveniles produced to the life-history strategy, for example, in *Adamietta* and *Brotia* among Pachychilidae. In con-

trast, the thiarids *Melanoides tuberculata*, *Thiara scabra* and *Tarebia granifera*, where by comparison relatively few but well developed juveniles hatch, exhibit the so-called "k-strategy", as it is also found in *Tylomelania* and *Pseudopotamis* among pachychilids.

CONCLUSION

It is common knowledge among malacologists that viviparity has evolved repeatedly and independently in limnic gastropods and bivalves. However, as is revealed from our new systematization of limnic Cerithioidea, live-bearing strategies have evolved along independent evolutionary avenues even within this superfamily and within some of its constituent families. Furthermore, the morphological structures involved and reproductive strategies realized evolved repeatedly in parallel. Generally, in brooding gastropods uterine brood sacs are modified from the pallial section of the oviduct which can be found among Cerithioidea in the Paludomidae, Pachychilidae and Pleuroceridae. In contrast, subhaemocoelic brood pouches derived convergently at least in the marine Planaxidae, some SE Asian Pachychilidae and the Thiaridae s. str., while the mesopodial brood pouch of the Tanganyikan paludomid *Tanganyicia rufofilosa* is certainly a structure that evolved independently yet again.

Although a uterine viviparous strategy is found in lacustrine genera and species from Lake Tanganyika (*Lavigeria*, *Tiphobia*), in Japanese Lake Biwa (*Semisulcospira*) and the Central lakes on the Indonesian island Sulawesi (*Tylomelania*), this mode beyond doubt evolved several times in parallel, too. However, earlier and often repeated assumptions and scenarios (e.g. in Boss, 1978; Calow, 1978; Michel, 1994) proposing that viviparity has a causal link to the colonization of limnic habitats and with speciation, adaptive radiation and dispersal are ill-founded. Particularly, its role in speciation as an intrinsic and ultimate factor remains to be carefully evaluated in lacustrine and riverine case studies. For example, for limnic SE Asian Pachychilidae we hypothesized that viviparity has evolved in species that already had colonized fresh water (see Köhler et al. 2004). Consequently, in this case at least the development of breeding was not correlated with the colonization of this new ecological zone.

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