ONTOGENETIC CHARACTERS OF MYTILACEANS

By Kurt Ockelmann
Marine Biological Laboratory, Strandpromenaden, 3000 Helsingør, Denmark

ABSTRACT

Characters of mytilids are summarized. Ontogeny of the mytilid shell and hinge are illustrated. Main musculature and scars on the inside of the shell are exemplified and illustrated by *Perna viridis* (L.).

INTRODUCTION

Some mytilid lineages are rather conservative while others show a high degree of convergent or parallel evolution. Earliest fossil records are from the Devonian. The taxon may be much older, however. The "archetype" lived in shallow, marine, probably fairly warm water under conditions of moderate water motion. Probably, it lived epifaunally, byssally attached, and nestling. The "archetype" was suspension feeding on nano- and microfractions of seston, and its larvae were planktotrophic.

Modern mytilids are widely distributed from arctic to tropical zones and from the intertidal to the abyssal. Some have even become adapted to a life in freshwater. Many species are small and their biology is hardly known (Ockelmann 1983). In comparison, other species have been intensively studied; above all *Mytilus edulis* which appears to be the most studied of all molluscs. Its filter-feeding and growth have been much studied (cf. Jørgensen 1990). It has been widely used for eco-physiological experiments, feeding behaviour (Bayne et al, 1989), biodeposition, and modelling of optimal foraging theory (Bayne et al. 1976; Jørgensen 1990). It has been used in environmental monitoring programmes as the "mussel watch" (Riisgaard *et al.* 1987; Jørgensen 1990), and it is an important commercial species which is collected by hand, trawled or grown in culture.

The purpose of this short contribution is to summarize and to point out important taxobases for the study of mytilids. During my work with identification of the mytilids of the Zoological Museum, University of Copenhagen, I found that systematic treatment of the species requires some comments and explanations because there is no consensus in the existing literature regarding terminology (Ockelmann 1983). I also include some original drawings pointing out developmental stages and the scars to be found where soft parts had been attached to the adult shell of *Perna viridis*.

ONTOGENY OF MYTILIDS

Basically, the shell ontogeny of mytilids comprises four stages referred to as prodissoconch I, prodissoconch II, nepioconch, and dissoconch. The first two stages occur before metamorphosis, while the latter two are normally formed after metamorphosis or hatching (in case of direct development). Byssus glands are functional well before metamorphosis of the larvae.

Prodissoconch I: This stage is an embryonic formation. It is always found and measures usually about 0.1 mm. It is clearly seen in species with planktotrophic development (Fig. 1 A) but may be less distinctly limited in species with lecithotrophic development. There is a very close size relationship between the prodissoconch I and egg size (Ockelmann 1965).
Prodissoconch II: This is a larval formation. The stage measures about 0.3 mm in most species with planktotrophic development (Fig. 1 B), but it may be reduced or absent in species with lecithotrophic development. Late veliconchae (or prodissoconchs II) are oblong-triangular in side view, resembling arcacean larvae in certain musculines, while in, *e.g.*, *Mytilus* and *Modiolus* they are rounded-triangular. One pair of visceral eyes is present.
Nepioconch: This is a juvenile shell stage. A well-defined nepioconch is produced by many mytilids (Fig. 1 C). It is distinguished by shell texture, shape, hinge characters and usually also by sculpture and colouration. It should be noted that the nepioconch mistakenly has been referred to as "prodissoconch" in

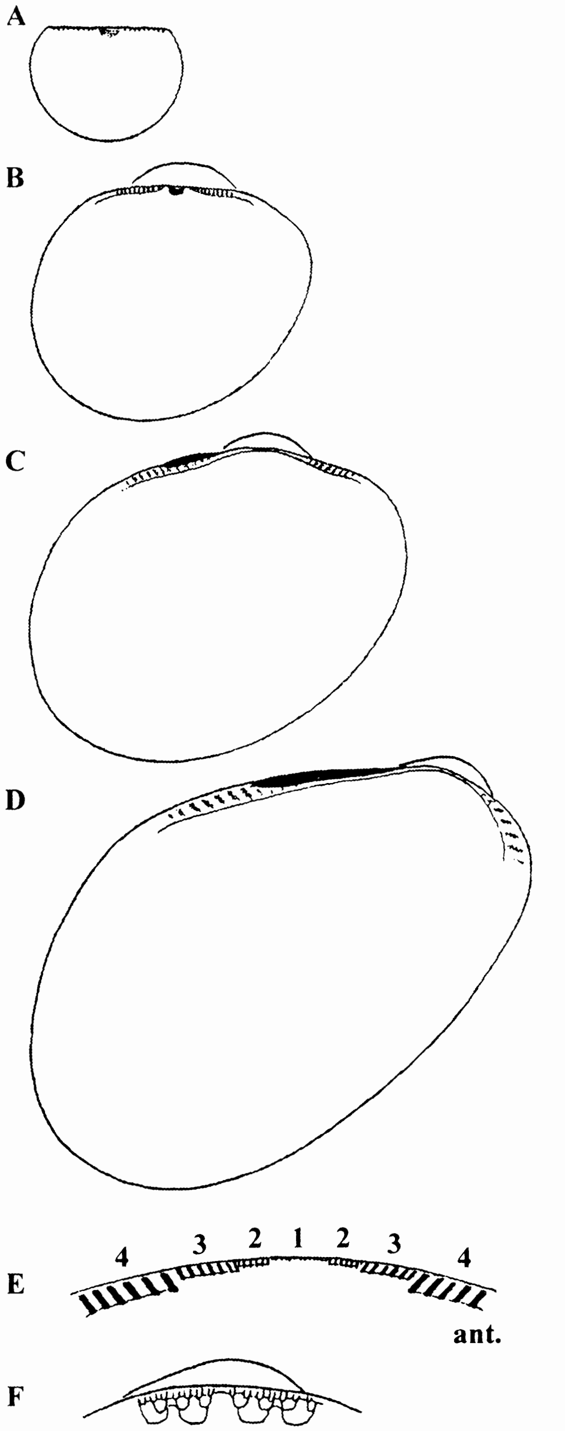

Figure 1. (A) prodissoconch I. (B) prodissoconch II. (C) nepioconch. (D). dissoconch. (E) scheme of sequence of all 4 series of hinge teeth. (F) growth and modification of hinge teeth, originating from series 2 and 1.

part of the literature. This is unfortunate. The nepioconch is a well defined stage which is a generally useful taxonomic tool, although it has been lost in several mytilid taxa.

Dissoconch: This is the adult stage where the final characters are developed. In young adults, the hinge teeth may often be seen even if the teeth are lost in fully grown adults (Fig. 1 D).

Hinge teeth: Fig. 1(E) shows a scheme of the sequence of the four possible series of hinge teeth which may develop in mytilids. Teeth are formed by iteration in corresponding series anteriad and posteriad. Series (1) and (2) may not be clearly separate. The anterior series (3) is rare. In comparison series (1 + 2) are always for-med. The posterior series (4) may or may not remain functional in the adult stage.

It is taxonomically and phylogenetically important that there exist considerable differences between genera as to the ontogeny of these hinge elements. Thus, *e.g.*, in *Mytilus edulis*, series (3) is not formed at all, and of series (4) only the anterior portion is found in the adult stage, while in *Modiolus modiolus* series (1, 2, and 3) occur in the ontogeny, while series (4) has completely been lost and there are no so-called dysodont teeth in the hinge of the adult horsemussel. Besides, *Mytilus* spp. lack a nepioconch whereas all *Modiolus* spp. do form one. Probably, separation between these superficially similar genera occurred already in the Palaeozoicum.

Fig 1 (F) shows growth and stepwise modification of series (2) with (1). This process of hinge teeth formation is typical of several genera, *e.g.*, it is very clearly shown by *Brachidontes* and *Septifer*.

Ligament: Most mytilids develop two distinct ligaments in ontogenetic sequence. They develop separately. The primary ligament is internal, and formed at, or slightly behind, the centre of the provinculum of embryonic or larval prodissoconchs (Fig. 1, A & B). After metamorphosis (or hatching) an external secondary ligament becomes functional. This opisthodetic, parivincular ligament is separate from the internal larval ligament and will overgrow the function-less hinge teeth (Fig. 1, C & D). In a few genera (*Perna*, *Xenostrobus*) the parivincular ligament appears already in the larvae before metamorphosis. The primary ligament remains functional in the adults of very few mytilid genera, *e.g.*, in *Dacrydium*, where a weak secondary ligament appears very late in ontogeny or not at all (Ockelmann 1983).

CHARACTERS OF ADULT MYTILIDS

Shell: The "archetype" was small to medium sized, rather thin with a fine radial sculpture and probably also fine commarginal ridges. Colour pattern showed wavy bands, brown, red, or lilac, crossing the growth lines. Shell shape was equivalve, inequilateral, widely rounded anteriorly, somewhat expanded posteriorly.

Some mytilid taxa carry so-called "periostracal hairs" during most of their life, while other taxa have "hairs" only when they are juvenile, but not as adults. *Mytilus edulis* is an example of the latter condition. The "hairs", however, are not true parts of the periostracum. The mussel's foot and the associated complexes of glands produce the "hairs" which are deposited on the outer shell surface. Newly produced hairs are easily recognized due to their pale colour. Because of their origin, I recommend to use the term "byssal hair, bristle, or special secretion" for these projections on the periostracum. The Mytilacea are among all bivalves outstanding with respect to the great importance of byssus secretions (and the glands producing them). They may be used not only for attachment to a firm substratum, but also for nest-building, protection or defense by means of byssal hairs and/or secretions glueing foreign objects to the shell outside, and even for postlarval transport in certain spp. paralleling the method used by newly hatched spiders.

Anatomy: The adductor muscles were originally nearly equal in size (almost isomyarian) in the mytilacean "archetype" and during early stages in ontogeny. The heteromyarian condition develops later and is secondary. Fig. 2 shows the main musculature and scars inside the shell of *Perna viridis*. Mytilids have two pairs of filibranch demibranchs, the outer pair shorter anteriorly. Pedal gape and the inhalant opening are separated. An exhalant siphon is present. Muscular lobes of the mantle margin are plain, and sensory lobes simple. The foot is well developed for creeping and attachment aided by byssus glands. The "archetype" had probably more than two pairs of byssus retractor muscles, and the visceral eyes were persisting. They are lost in a few extant genera. Fig. 2 shows the posterior byssus retractor muscles of *Perna viridis* divided into two portions (No. 7) and the anterior byssus retractor muscle (No. 13).

In the adult *Perna*, the loss of the anterior adductor muscle is remedied for by the 1-2 strong "dysodont" teeth in each valve and by the fused and strong periostracum ventrally. Separation of the umbones as a consequence of shell growth is also remedied by sealing the gape with fused periostracal matter.

Reproduction: Sexes are separate in the majority of mytilids as is free spawning of the gametes. Most mytilids have a planktotrophic development but lecithotrophic development, whether including a larval phase or being direct, is found in several taxa. The infaunal genus *Crenella*, *e.g.*, deposits egg masses in an exhalant tube produced by the foot.

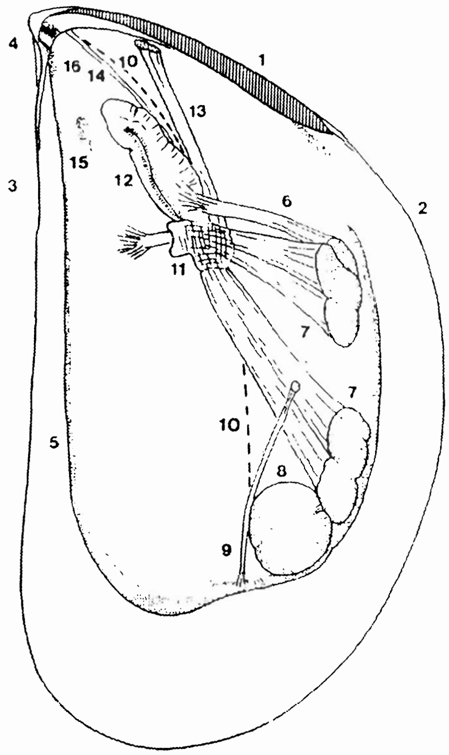

Figure 2. *Perna viridis* (L.). Main musculature and scars (dotted) on inside of right hand valve. (1) ligament. (2) end of fusion of periostracum and of middle fold. (3) byssus gape. (4) tooth. (5) pallial line (dotted). (6) elevator pedis muscle. (7) posterior byssus retractor muscle. (8) posterior adductor. (9) ctenidial muscle. (10) lower trajectory of posterior adductor. (11) foot base and byssus complex. (12) foot. (13) anterior byssus retractor muscle. (14) palp suspensor muscle. (15) attachment scar of outer labial palp. (16) scar after now lost anterior adductor

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