ONTGENETIC CHARACTERS OF MYTLACEANS

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ABSTRACT

Characters of mytilids are summarized. Ontogeny of the mytilid shell and hinge are illustrated. Main muscles, mantle, 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 taxa may be much older, however. The "archetypic" lived in shallow, marine, probably fairly warm water under conditions of moderate water motion. Probably, it lived epifaunally, byssally attached, and nesting. The "archetypic" was suspension feeding on nano- and microcrustaceans, and its larvae were planktotrophic.

Modern mytilids are widely distributed from arctic to tropical zones and from the intertidal to the abyssal. 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 (e.g., Jorgensen 1990). It has been widely used for eco-physiological experiments, feeding behaviour (Bain et al., 1989), biodeposition, and modelling of optimal foraging theory (Bain et al. 1976; Jorgensen 1990). It has been used in environmental monitoring programmes as the "module watch" (Risgaard et al. 1987; Jorgensen 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 observations for the study of mytilids. During my work with identification of the molluscs at 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.

ONTGENSY OF MYTIIS

Basicall, the shell ontogeny of mytilids comprises four stages referred to as primisocuschol, prodiosicoschol, and disoicoschol. 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 larva.

Prodissicoschol 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 prodissicoschol I and egg size (Ockelmann 1965).

Prodissicoschol 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 velerontene (or prodissicoschols II) are oblong-triangular in side view, resembling mythisan larvae in certain molluscs, while in, e.g., Mytilus and Modiolus they are rounded-triangular. One pair of visceral eyes is present.

Neipicoschol: This is a juvenile shell stage. A well-defined neipicoschol is produced by many mytilids (Fig. 1 C). It is differentiated by shell texture, shape, hinge characteristics and usually also by sculpture and coloration. It should be noted that the neipicoschol mistakenly has been referred to as "prodissicoschol" in
part of the literature. This is unfortunate. The nepicoch conch is a well defined stage which is a generally useful taxonomic tool, although it has been lost in several mytid taxa.

**Dissococonch:** This is the adult stage where the final characters are developed. In young adults, the hinge teeth may 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 mytids. Teeth are formed by iteration in corresponding series interradial and posterior. 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 ontology 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 horse mussel. Besides, *Mytilus* spp. lack a nepicoconch whereas all *Modiolus* spp. do form one. Probably, separation between these superficially similar genera occurred already in the Palaeozoic.

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 closely shown by *Brachidontes* and *Septifer.*

**Ligament:** Most mytids develop two distinct ligaments in ontogenetic sequence. They develop separately. The primary ligament is internal, and formed as or slightly behind, the centre of the proloculum of embyronic or larval prodisococonchs (Fig. 1, A & B).

After metamorphosis (or hatching) an external secondary ligament becomes functional. This epipodial, parvicular 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 parvicular ligament appears already as the larva before metamorphosis. The primary ligament remains functional in the adults of very few mytid genera, e.g., in *Dacytium,* where a weak secondary ligament appears very late in ontogeny or not at all (Ockelmann 1983).

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**Figure 1.** (A) prodisococonch I. (B) prodisococonch II. (C) nepicoch. (D) dissococonch. (E) scheme of sequence of all 4 series of hinge teeth. (F) growth and modification of hinge teeth, originating from series 2 and 1.
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 patterns showed wavy bands, brown, red, or lilac, crossing the growth lines. Shell shape was ovate, inequilateral, widely rounded anteriorly, somewhat expanded posteriorly.

Some mytilids, e.g., 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 complex of glands produce the "hairs" which are deposited on the outer shell surface. Newly produced hairs are easily recognized due to their pale color. Because of their origin, I recommend to use the term "byssus 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 via means of bivalve hairs and/or secretions gluing foreign objects to the shell outside, and even for postlarval transport in certain spp. parallelizing the method used by newly hatched spiders.

Anatomy: The adductor muscles were originally nearly equal in size (almost bonyward) 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 sears inside the shell of Perina 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 Paxiidae genera. Fig. 2 shows the posterior byssus retractor muscles of Perina viridis divided into two portions (No. 7) and the antero-lateral byssus retractor muscul (No. 13).

In the adult Perina, the loss of the anterior adducti muscle is remedied for by the 1-2 strong "chordale" 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 setting 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. Perina viridis (L.). Main musculature and scars (shown) on inside of right hand valve. (1) ligament. (2) end of byssus of periostracum and of middle fold. (3) byssus gape (4) tooth. (5) palial line (dotted). (6) elevator pedis muscle. (7) posterior byssus retractor muscle. (8) posterior adductor. (9) sternal muscle. (10) lower trajectory of posterior adductor. (11) tooth base and byssus complex. (12) base. (13) anterior byssus retractor muscle. (14) palp suspensormuscle. (15) attachment musc of outer lateral palp. (16) scar after removal anterior adductus adduction.
REFERENCES


