

# PART N, REVISED, VOLUME 1, CHAPTER 4: THE EARLY SHELL: ONTOGENY, FEATURES, AND EVOLUTION

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## INTRODUCTION

All bivalves go through a succession of two or more shell-forming phases before the adult valves take shape. These early, larval to juvenile portions of the shell, and their morphology, morphogenetic patterns, taxonomic distribution, and evolutionary interpretations are the subjects of this chapter. Some aspects of the processes of shell formation at the level of cell lineages and control genes are briefly summarized. Most research conducted on these topics focuses on phases preceding the veliger and pericalymma larvae. However, from a morphological perspective, the most instructive modifications occur around the metamorphic window, where shell features are most diverse and record differences in reproductive modes and heterochronic changes. These changes provide clues to the evolution of autobranchs and protobranchs. The following sections are dedicated to establishing a theoretical framework for interpretation and defining the essential terms.

## BASIC CONCEPTS AND SHELL TERMS

### CONTINUOUS ONTOGENY AND STAGED DEVELOPMENT

Bivalves are said to have a biphasic (larval, postlarval) life cycle, which suggests a complete disruption of ontogeny. However, NAEF (1919, p. 17) and, more recently, HICKMAN (1995, 1999) and PECHENIK (2006) have stressed that ontogeny is a continuous process consisting of alternating phases of slow(er) and fast(er) development (cf. HICKMAN, 1999, p. 27). It is assumed here

that the embryonic, larval, metamorphic, and postlarval (juvenile to adult) phases represent major developmental alternations in this sense. The term phase is herein restricted to refer to a certain developmental period.

Comparisons between developmental trajectories of organisms require reference points marking the onset and offset of phases. Traditionally, these boundaries have been defined on the basis of morphologically recognizable markers, such as the appearance and disappearance of organs or, in the case of molluscan shell development, changes in structure, sculpture, or direction of growth. The term stage is herein restricted to refer to these morphologically recognizable units of the shell.

Defining clear reference points for ontogenies is important because onsets, offsets, and development rates can vary among organs of a species as well as among homologous organs in distinct species (heterochrony). This may lead to conflicting concepts of developmental phases. For example, GROS, FRENKIEL, and MOUËZA (1997) observed differences in the early development of gills, siphonal structures, and shells of various heterodont bivalves with similar reproductive modes. Their observations led them to distinguish two metamorphic phases, late larval and early postlarval, and to raise the question of which criterion should be used to mark the offset of the larval phase. Shell development is similarly diverse, including discrete shell stages within both larval and postlarval phases, dislodgements of shell features between one and the other phase, or continuity of development beyond metamorphosis.

For the purposes of this chapter, we will consider the end of the larval phase as being marked by the disappearance of the pericalymma in the Protobranchia and the velum or its homologous cephalic mass (OLDFIELD, 1964, p. 91) in the Autobranchia. The subsequent juvenile phase is then the period during which metamorphosis of some organs may continue until the organism becomes reproductively mature. The first metamorphic event typically correlates with a marked change from larval to postlarval shell morphology. Thus, the resulting shell boundary may be taken as a relatively good proxy for the end of the larval phase. Postlarval shell development also typically records at least one morphological stage, and sometimes more, before the final stage is reached. These earlier stages are here attributed to the juvenile phase. However, whether or not the last change corresponds to the adult, sexually mature phase has yet to be proven. Note that the shell stages described below are primarily defined by morphological differences, and not all stages are present or observable in all bivalves. This may be a consequence of the genetic program, reproductive mode, or extrinsic factors.

#### HISTORICAL REVIEW OF BASIC SHELL TERMS

Henri de LACAZE-DUTHIERS (1856) was the first to observe that bivalve larvae and postlarvae (in *Mytilus edulis* LINNAEUS, 1758) display distinct shell morphologies. Much later, JACKSON (1890, p. 281) coined the terms prodissoconch and dissoconch for these shell stages. His choice of names was intended to reflect presumed homology with the protoconch and conch (later called teleoconch) of other mollusks and at the same time recall their distinctive, two-valved nature. Whereas prodissoconch has become the standard term for the larval bivalve shell (although protoconch is preferred by some authors), dissoconch is used less often. Felix BERNARD (1896a, p. 56) subsequently noted that the prodissoconch itself consists of two substages, which he called prodissoconch

primitive and prodissoconch definitive. Since WERNER (1939, p. 9), these substages have been referred to as prodissoconch I and II (originally Prod. I and Prod. II), terms that have been abbreviated to P I and P II (or Pd I, Pd II) by later authors. More recently, MALCHUS and WARÉN (2005) suggested the use of P-1 and P-2, in analogy with ligament 1 and ligament 2 (L1, L2) (cf. BERNARD, 1896b, p. 416, fig. 1), to avoid confusion with similar abbreviations (e.g., posterior lateral/lamellar teeth). The new *Treatise* glossary suggests using prodissoconch-1 and prodissoconch-2 (P-1, P-2), which is followed here (CARTER & others, 2012; Fig. 1).

The terms nepioconch and mesoconch were introduced by WRIGHLEY (1946, p. 14–15) to distinguish the earliest postlarval (juvenile) and following intermediate stages before the adult stage. The term nepionic had already been proposed by A. HYATT (in JACKSON, 1890, p. 290, footnotes 1–2), but that term was ignored by subsequent authors. The term interdissoconch of JØRGENSEN (1946) is equivalent to the nepioconch. WRIGHLEY's (1946, p. 14–15) original description of the nepioconch of Tertiary *Caestocorbula costata* (T. BROWN, 1849 in 1837–1849) and *Callocardia nitidula* (LAMARCK, 1806 in 1802–1806), appears ambiguous because most of the listed attributes (e.g., “perched on apex,” and “margin distinctly raised from succeeding shell”) could also apply to the prodissoconch. However, the reported sizes of 8 mm and 6 mm, respectively, are too large for a larval shell. GOODWIN, ANDERSON, and ROOPNARINE (2008) recently provided more explicit evidence for ontogenetic and phylogenetic growth variations in Corbulidae, which in some groups include development of a distinct nepioconch.

Some bivalves develop a narrow shell rim at the boundary between the prodissoconch and nepioconch. This feature, presently called the metamorphic (shell) lip (Fig. 1), may correspond to shell added during the settling phase (spat of GOODWIN, ANDERSON,

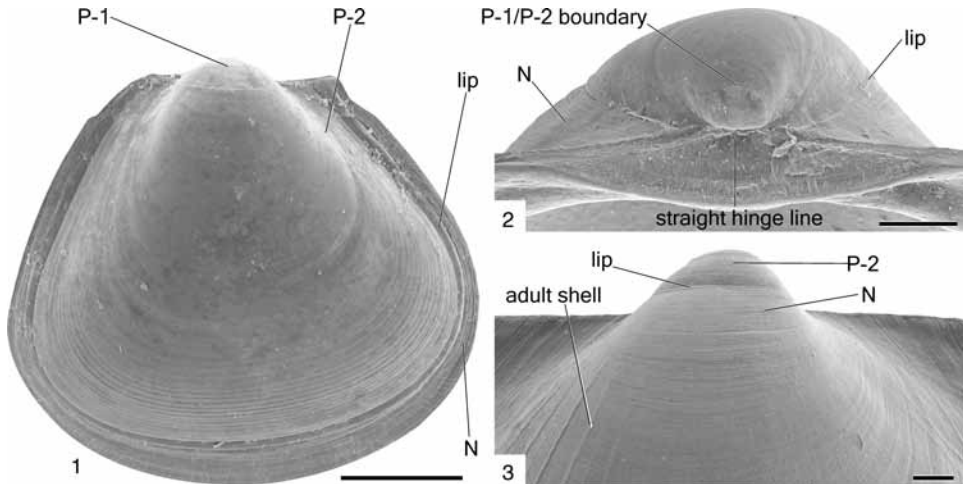


FIG. 1. Scanning electron micrographs of *Limaria loscombi* (G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834), showing the basic early ontogenetic shell stages of bivalves, prodissoconch-1 and prodissoconch-2 (P-1, P-2), nepioconch (N), and adult shell; note metamorphic shell lip marking boundary between prodissoconch and nepioconch; 1, early juvenile; 2, hinge and umbonal area; 3, external view of umbonal area; scale bars, 100  $\mu\text{m}$  (new).

& ROOPNARINE, 2008). For simplicity, this substage is considered part of the nepioconch.

The hatched or released shell stage of taxa with encapsulated eggs or brood protection has been commonly referred to as larval shell in the literature. In numerous instances, however, the hatched or released animal is a postlarva, already displaying some nepioconch growth. Two new terms are introduced herein to address this problem: (1) metaconch is the postlarval shell stage in which the boundary between nepioconch and prodissoconch is discernible on release from the mother or egg capsule; (2) cryptoconch is the shell stage in which the limits between the earliest stages P-1, P-2, or nepioconch, cannot be clearly recognized on release from the mother or egg capsule. This includes shells in which a well-defined morphological boundary could be interpreted either as prodissoconch-1/2 or as P-2/nepioconch. With better knowledge, researchers should be able to identify cryptoconchs as either prodissoconchs or metaconchs.

The term early ontogenetic shell is used here as a descriptive term applicable to any

shell stage formed before the onset of the adult shell. Some terms pertaining to developmental phases and stages are presently used in a restricted sense or avoided for being synonymous or unclear. For example, the term embryo has been defined morphologically and ecologically. Because ecological definitions of embryo include any phase before hatching from the egg or release from the mother (cf. TURNER, PECHENIK, & CALLOWAY, 1987), the term embryonic shell of authors may refer to any premetamorphic or early postmetamorphic shell stage [e.g., BERNARD'S (1895, p. 108, fig. 1) embryonic dissoconch]. To avoid mixing concepts herein, we define presently adopted phase names—e.g., gastrula, trochophore, veliger, and pericalymma—in a purely morphological context and restrict the term embryo to the phases up to and including the gastrula, after which the premetamorphic animal is considered a larva.

Although BANDEL (1988), following FIORONI (1966), suggested the term preveliger, rather than a (late) trochophore, to describe the organism developing a shell field, this terminology is not currently

followed because shell field ontogeny begins much earlier (e.g., MOUÉZA, GROS, & FRENKIEL, 2006; KIN, KAKOI, & WADA, 2009) and the term intrinsically excludes protobranchs and unionoids. BANDEL (1988) termed the first and purely organic univalve of this phase the primary shell (more commonly called the pellicle) and the first mineralized shell the secondary shell, corresponding to the P-1 and possibly also P-2 in the present terminology (cf. BANDEL, 1988, p. 242–243).

The veliconcha of various authors includes both the prodissoconch-1 and prodissoconch-2 stages, whereas D-shaped (straight-hinge) and umbonate veligers refer to certain shell outlines of veliger larvae. D-shaped outlines span the P-1, P-2, and sometimes the nepioconch stages, whereas many veliger shells are not umbonate. In addition, all three so-called pseudostage names apply only to non-unionoid autobranchs. Such references to specific shell outlines may comprise useful shape descriptors, but they are unwarranted for defining shell stages.

KŘÍŽ (1979, 1985, 2007) used another system to address morphological shell stages, which he numbered Stage I through Stage V. Unfortunately, the early ontogenetic shell boundaries in the Silurian taxa for which these stages were devised must be inferred from internal molds, hampering unambiguous correlations with the present scheme for living bivalves. Most likely, his Stage I corresponds to P-1+P-2 (sometimes perhaps including the nepioconch) (cf. KŘÍŽ, 1979, p. 30, fig. 16); Stage II is either the nepioconch or includes both nepioconch and mesoconch; Stage III is unnamed here; Stage IV is the adult; and Stage V the gerontic shell of KŘÍŽ (not presently distinguished) (cf. KŘÍŽ, 2007, fig. 11).

## SHELL DEVELOPMENT

Very little is known about the process of earliest bivalve shell development at the level of cell lineages. This is especially true for protobranchs, where the cell-test around the developing animal prohibits direct observation. The following section briefly reviews

the essential steps, contrasting them with evidence from molecular developmental studies and morphological growth patterns of the shell.

## SHELL FIELD AND PELLICLE

Shell formation in autobranchs seems to begin late in the gastrula with the differentiation of a specialized region of the embryonic ectoderm, the shell field (shell gland in older literature), which secretes the shell (WALLER, 1981, and references therein; MOUÉZA, GROS, & FRENKIEL, 2006). Due to its function, WALLER (1981) and BANDEL (1988) considered the shell field as a precursor of the mantle. Observations of the planktotrophic venerids *Anomalocardia brasiliiana* (GMELIN, 1791 in 1791–1793) and *Chione cancellata* (LINNAEUS, 1767 in 1766–1767) by MOUÉZA, GROS, and FRENKIEL (1999, 2006) suggest that the shell field begins to differentiate in a weak depression of the apical portion of the gastrula. Continuous growth around the shell field leads to its partial overgrowth by prototroch cells (Fig. 2.1). This phenomenon was previously described as an invagination, based on a process observed in gastropods, but this was criticized by BANDEL (1988) and MOUÉZA, GROS, and FRENKIEL (2006). BANDEL'S (1988, p. 242) hypothesis that the shell gland may have been confused with the rudimentary cells of the hind gut and anus cannot be substantiated. Instead, the more recent literature suggests that the development of the shell field in bivalves is rather variable (e.g., EYSTER & MORSE, 1984; EYSTER, 1986; BANDEL, 1988; MOUÉZA, GROS, & FRENKIEL, 2006). Within hours, the shell field cells, termed T1 cells by MOUÉZA, GROS, and FRENKIEL (2006), begin to secrete the rudiment of the periostracum or pellicle, which is still undivided and later serves as a substrate for deposition of the shell.

## SADDLE-LIKE PERIOSTRACUM AND PRODISSOCONCH-1

Lateral expansion of the organic pellicle over the embryo gives rise to a saddle or

dumbbell-shaped valve with a straight middle line defining the future hinge (Fig. 2.1–2.2). According to observations in *Chione cancellata* (LINNAEUS, 1767 in 1766–1767), the hinge line is produced by a new cell type, T2, pushing the apical T1 cells apart and generating the first ligament (cf. MOUËZA, GROS, & FRENKIEL, 2006). At the same time, cells of a third type, T3, differentiate between adjacent T1 cells in both the left and right lobes of the shell field. During further growth of this saddle-like shell field, the embryo becomes laterally compressed (Fig. 3). Shell mineralization begins after the periostracum encloses the larva, and the T3 cells have produced a second organic layer, which will envelope crystals of calcium carbonate. In the first phase, amorphous calcium carbonate (ACC) is deposited, which transforms into aragonite granules embedded in the organic matrix (WEISS & others, 2002). The result of this process is a calcified bivalved shell, the prodissoconch-1, characterized by a straight hinge (Fig. 1.2, Fig. 4.1). The center of each P-1 valve, where shell mineralization begins, is termed cicatrix. The cicatrix is often depressed and usually displays small pits and wrinkles, but these may be less obvious or lacking if the periostracum is worn (Fig. 4.2–4.3; see Fig. 10.1–10.2; CARTER & others, 2012, fig. 250). According to BANDEL (1982, p. 140), the stress field (wrinkles, folds) in the cicatrix are produced by muscles pulling the still uncalcified or weakly calcified valves together (pits represent the traces of the muscle field). Such muscle traces may be poorly developed, and their position and number may be rather variable within the cicatrix.

P-1 development in protobranch bivalves is very poorly known but supposedly proceeds in a similar fashion. Most protobranchs do not calcify their shell before metamorphosis (GUSTAFSON & REID, 1986; GUSTAFSON & LUTZ, 1992; ZARDUS & MORSE, 1998; ZARDUS, 2002). However, if the early mineral phase is ACC, then calcification may have been overlooked, as older

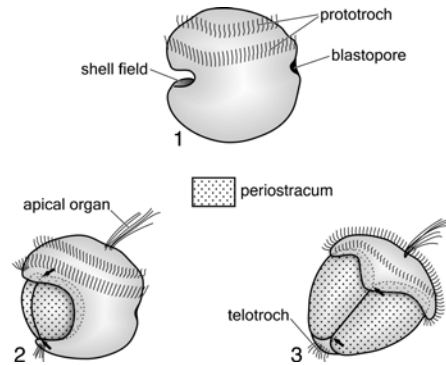


FIG. 2. Shell development in *Chione cancellata* (LINNAEUS, 1767 in 1766–1767), from gastrula (1) to trochophore (2–3); 1, dorsolateral view of young gastrula (6 hours after fertilization), showing shell field expanding below the prototroch; 2, dorsolateral view of a trochophore (12 hours after fertilization), showing gradual expansion of pellicle, secreted by the shell field and separated in two valves by the hinge line (arrows), over the still nearly spherical body of the larva; 3, dorsal view of late trochophore (15 hours after fertilization), showing uncalcified valves now enclosing the soft body almost completely, compressing the larva laterally (adapted from Mouëza, Gros, & Frenkiel, 2006).

studies determined early shell mineralization indirectly by birefringence under polarized light and ACC has very low birefringence (WEISS & others, 2002).

The general scenario outlined above appears to be applicable to all bivalves. Most authors agree that the shell field periostracum detaches from the underlying cells before mineralization starts. MOUËZA, GROS, and FRENKIEL (2006) state that the T3 cells shed a second organic layer before mineralization; this is probably compatible with the above interpretation.

Histological and ultrastructural results are generally in good agreement with molecular analyses that demonstrate that the developmental regulator genes engrailed (EN) and decapentaplegic (Dpp) play an important role in molluscan larval shell development (WRAY & others, 1995; cf. GIBERT, 2002, regarding the wider distribution of these genes in the animal kingdom). The EN protein seems to set up the compartment boundary in which the shell field develops. Some studies also show that the EN protein is expressed within the

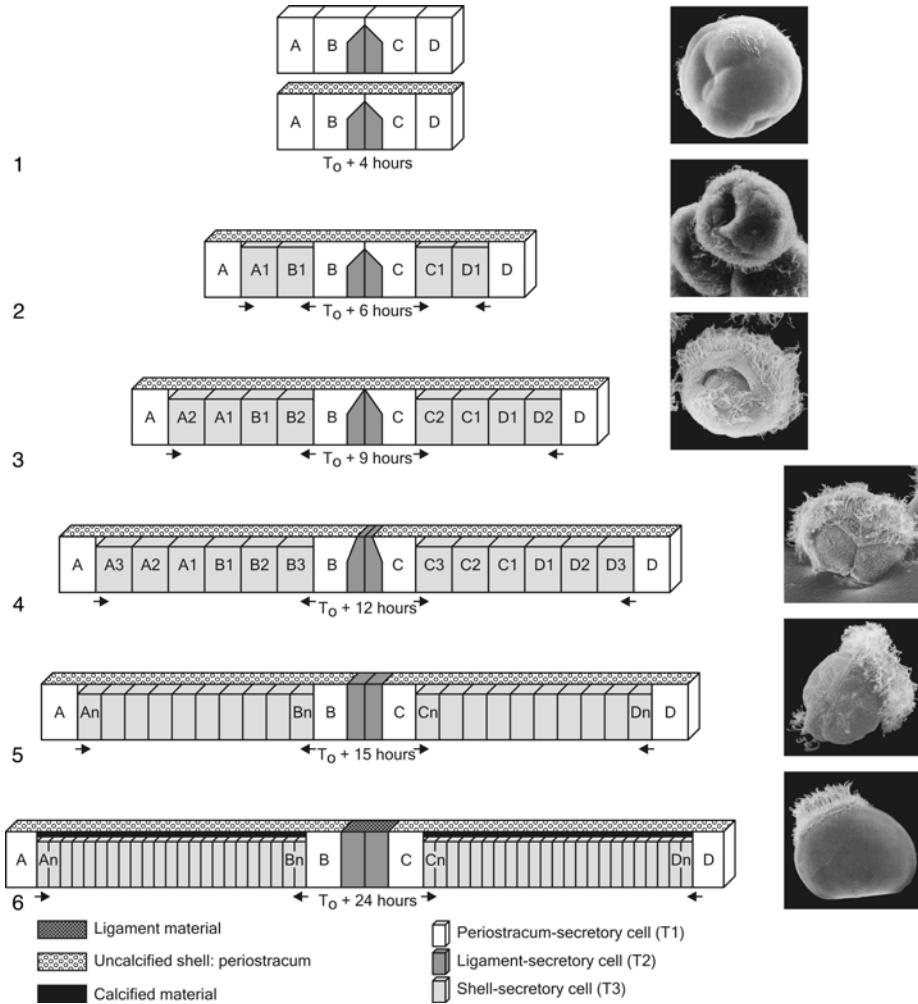


FIG. 3. Scanning electron micrographs and diagrammatic cross sections through shell field of *Chione cancellata* (LINNAEUS, 1767 in 1766–1767) at successive ontogenetic stages, providing a summary of shell development from gastrula to D-stage veliger; 1, 4 hours after fertilization ( $T_0 + 4 h$ ), the shell field comprises both periostracum (pellicle) and ligament secretory cells, the apical pole of the latter (T2 cells) being covered by the former (T1) cells; 2–3, 6 hours after fertilization ( $T_0 + 6 h$  and  $9 h$ ), shell secretory cells (T3) are formed from the division of T1 cells; 4–5, 12 hours after fertilization ( $T_0 + 12 h + 15 h$ ), the ligament secretory (T2) cells reach the surface of the shell-field epithelium, set apart the T1 cells, and create the two valves of the bivalve shell; 6, at 24 hours after fertilization ( $T_0 + 24 h$ ), T2 cells are now secreting ligament material along the hinge, while T3 cells elaborate a secondary organic layer that encloses calcium crystals; the valves, now calcified, lose their wrinkled aspect (adapted from Mouřza, Gros, & Frenkiel, 2006).

shell field, though with less intensity, which may suggest it is itself involved in calcification (MOSHEL, SEVINE, & COLLIER, 1998; WANNINGER & HASZPRUNAR, 2001; NEDERBRAGT, VAN LOON, & DICTUS, 2002; BARATTE, ANDOUCHE, & BONNAUD, 2007; IJIMA & others, 2008;

KIN, KAKOI, & WADA, 2009; ZHOU & others, 2010, in *Pinctada* RÖDING, 1798). Dpp (decapentaplegic) seems to delimit the extension of EN (engrailed) and, thus, the shell field. It has also been shown to be concentrated in the hinge area before and after the early

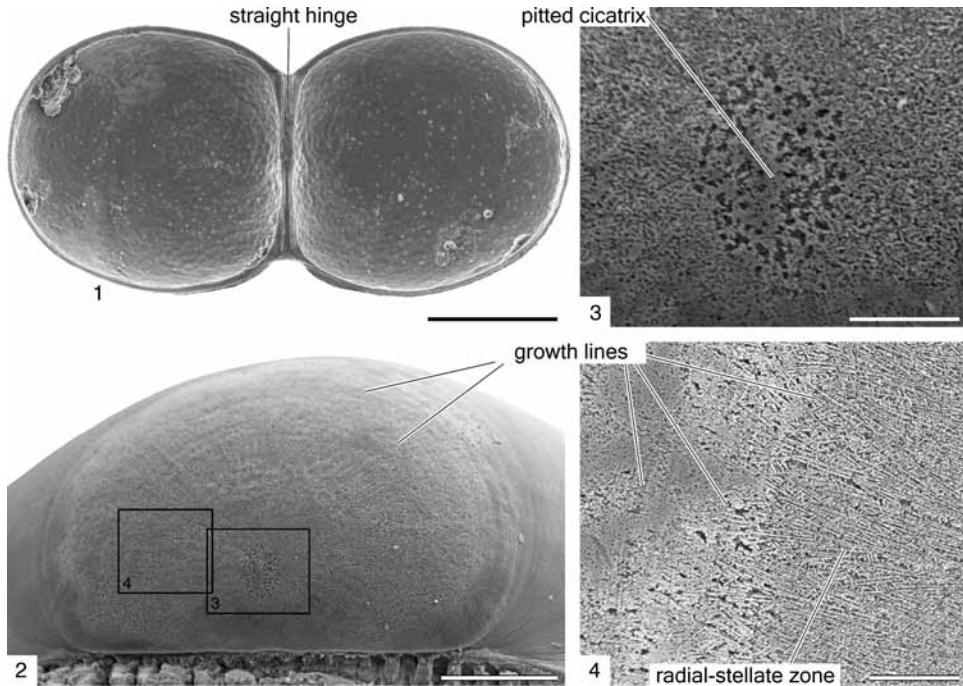


FIG. 4. Scanning electron micrographs of larval and early postlarval shells of autobranchs; 1, *Potomida littoralis* (CUVIER, 1798), internal view of prodissoconch-1, showing both valves divided by straight hinge line, scale bar, 100  $\mu\text{m}$  (Malchus & López, new); 2–4, *Musculus subpictus* (CANTRAINED, 1835); 2, commarginal growth lines on surface of the P-1, scale bar, 20  $\mu\text{m}$ ; 3, magnified view of area delimited by corresponding rectangle in view 2, showing pitted sculpture of cicatrix, scale bar, 5  $\mu\text{m}$ ; 4, magnified view of area delimited by the corresponding rectangle in view 2, showing details of radial-stellate microstructure, scale bar, 5  $\mu\text{m}$  (new).

mineralization, suggesting that it is involved, at least indirectly, in the formation of the flexible ligament (KIN, KAKOI, & WADA, 2009, in *Saccostrea kegaki* TORIGOE & INABA, 1981).

Results from MOUËZA, GROS, and FRENKIEL (2006) are consistent with shell growth patterns and allow for hypotheses on some unusual cases. The lasidium larvae of iridiniid unionoids, for example, develop a lobed but entirely uncalcified monovalve (BONETTO & EZCURRA, 1962, 1965). This suggests that T2 (ligament) and T3 (calcification) cells of the shell field are either inactive or do not differentiate in this group. Similarly, the accidental development of a calcified monovalve in the unionid *Anodonta cygnea* (LINNAEUS, 1758) (cf. BANDEL, 1988) could be attributed to a failure to produce T2 cells. An entirely different growth pattern is the incomplete, wheel-and-spoke-like, primary

calcification of the P-1 of *Condylocuna jimbecki* MIDDELFART, 2002b (and most likely other condylocardiids). The pattern may suggest a corresponding wheel-and-spoke-like distribution of T3 cells over the shell field or their asynchronous activation during the earliest shell-forming process. The fact that the space between the so-called spokes is later calcified argues for asynchronous activation.

Whereas the previous cases are comparatively rare, many autobranchs show very subtle commarginal growth lines on the advanced P-1 stage (possibly absent in proto-branchs). Growth lines indicate interruptions or severe reductions in the rate of shell secretion, which are typically related to the protraction and retraction of a free mantle margin. However, the mantle margin was probably not functional during P-1

formation (see next section, p. 8). Therefore, growth lines of the P-1 shell are more likely related to a progressive commarginal activation or development of T3 cells below a pre-existing periostracum, as in *Chione cancellata* (LINNAEUS, 1767 in 1766–1767) (MOUËZA, GROS, & FRENKIEL, 2006) and *Pteria penguin* RÖDING, 1798 (WASSNIG & SOUTHGATE, 2012). A comparable pattern would also arise if propagation of the periostracum and calcification proceeded synchronously over the larva until the mineralized shell could enclose its body. This hypothesis appears to be applicable to *Tridacna squamosa* LAMARCK, 1819 in 1818–1822, *Lasaea subviridis* DALL, 1899, and *Ostrea edulis* LINNAEUS, 1758 (LABARBERA, 1975; WALLER, 1981, p. 5; Ó FOIGHIL, 1986). In summary, it seems likely that P-1 shell growth patterns reflect cell lineage activations and possibly also EN and Dpp activation sites. Their distribution patterns should, therefore, be as diverse as the shell growth patterns themselves. Available data are still limited, however: JACOBS and others (2000) for *Transennella* DALL, 1883; KIN, KAKOI, and WADA (2009) for *Saccostrea* DOLLFUS & DAUTZENBERG, 1920 in 1902–1920; and ZHOU and others (2010) for *Pinctada* RÖDING, 1798; further studies are needed before a model of shell development can be devised that integrates observations at the morphological, cellular, and genetic levels.

### PRODISSOCONCH-2

P-1 formation ceases when further calcification proceeds exclusively at the periostracum edge, eventually leading to the growth of a second larval shell or prodissoconch-2. This stage is typically characterized by well-developed commarginal growth increments (Fig. 1.1). During its growth phase, the straight hinge differentiates into a provinculum, with hinge teeth and a socket for the larval ligament. The ultimate size and morphology of the P-2 are largely influenced by the developmental mode. *Planktomya* SIMROTH, 1896, is possibly the only auto-branch genus with a mineralized P-1 and an

apparently nonmineralized, periostracal P-2 (ALLEN & SCHELTEMA, 1972; GOFAS, 2000). Protobranchs lack the P-2 shell stage altogether (GUSTAFSON & REID, 1986; GUSTAFSON & LUTZ, 1992; OCKELMANN & WARÉN, 1998; ZARDUS & MORSE, 1998; ZARDUS, 2002).

P-2 shells are typically three layered, consisting of an outer prismatic, middle granular, and inner prismatic layer (WALLER, 1981; WEISS & others, 2002). As with the P-1, the prodissoconch-2 shifts in mineralogy from ACC to aragonite (WEISS & others, 2002). Evidence of this transition was possibly first recorded by LABARBERA (1975), who noted a gradual increase in birefringence in prodissoconchs of *Tridacna squamosa* (LAMARCK, 1819 in 1818–1822). However, LABARBERA regarded the change as an artifact of preparation. The mineral phase of prodissoconchs seems to be usually exclusively aragonitic, even for bivalves with an almost entirely calcitic postlarval shell, such as post-Triassic Ostreoida (STENZEL, 1964; CARRIKER & PALMER, 1979). However, YOKOO and others (2011) recently found evidence for calcite in a middle shell layer after the initial aragonitic larval shell in a pteriid.

The underlying processes leading to distinct P-1 and P-2 stages are still a matter of dispute. BERNARD (1896a, p. 56), WERNER (1939), OCKELMANN (1965), and others assumed that these stages reflect the (abrupt) transition from shell field to mantle-margin calcification. WALLER (1981, p. 5) suggested that the P-1/P-2 boundary “represents nothing more than the onset of valve closure,” and BANDEL (1988) accepted this view. However, if WALLER (1981) was correct, how could the similar protoconch 1-2 boundary in planktotrophic gastropods be explained? Due to this difficulty, we adopt the view herein that there is no causal relationship between shell closure and P-2 development.

According to BANDEL (1988), P-1 shell mineralization is necessarily preceded by the detachment of shell field cells from the periostracum, leaving only the margin of the shell field and mantle connected to the rim of the shell. BANDEL (1988) considered



this the essential step toward the onset of P-2 development. However, this model is only valid for taxa in which the organic shell already covers the larva prior to detachment and calcification, such as *Teredora* BARTSCH, 1921 (BANDEL, 1988, p. 222, phase 5A) and *Chione* MEGERLE VON MÜHLFELD, 1811 (MOUËZA, GROS, & FRENKIEL, 2006). In species of *Ostrea* LINNAEUS, 1758 (WALLER, 1981), and *Tridacna* BRUGUIÈRE, 1797 in BRUGUIÈRE & others, 1791–1827 (LABARBERA, 1975), P-1 calcification begins long before the onset of the P-2 stage, suggesting that detachment, calcification, and P-2 development are not necessarily in phase. Therefore, the critical moment for P-2 shell secretion appears to be when the mantle develops bilobed margins divided by the periostracal groove, as found in such advanced veligers as *Ostrea* (WALLER, 1981) and *Pecten* O. F. MÜLLER, 1776 (CRAGG, 2006) (see also CRANFIELD, 1974; CASSE, DEVAUCHELLE, & LE PENNEC, 1998). This hypothesis essentially coincides with the views of earlier workers.

Unfortunately, the histology of the developing mantle margin and the functional details around the P-1/P-2 border have been described only by CASSE, DEVAUCHELLE, and LE PENNEC (1998) in *Pecten maximus* (LINNAEUS, 1758). Studies of gene expression patterns of EN and Dpp in *Saccostrea kegaki* TORIGOE & INABA, 1981 (KIN, KAKOI, & WADA, 2009), and *Pinctada RÖDING*, 1798 (ZHOU & others, 2010), have so far excluded the P-2 stage. According to WANNINGER and HASZPRUNAR (2001), EN activity in the scaphopod *Antalis entalis* (LINNAEUS, 1758) ceases with metamorphosis, but this mollusk does not develop a P-2 stage. It remains unclear whether EN and Dpp in bivalves invariably become inactive (with respect to shell formation) at the P-1/P-2 boundary, at metamorphosis, or perhaps after the juvenile stage.

### NEPIOCONCH

The shell transition of metamorphosing protobranchs has not been studied in detail. In autobranchs, the nepioconch begins to

form after metamorphosis, first as a lining on the interior of the prodissoconch and then by accretional growth. Provinculum growth may continue into this stage and beyond (see sections on the development of ligament and hinge teeth, p. 28–50, herein).

The newly formed shell is typically characterized by an abrupt increase in microstructural and ultrastructural complexity (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 12, Evolution of Bivalve Shell Microstructure, for further discussion). Shell tubules appear for the first time at this stage (REINDL & HASZPRUNAR, 1995; MALCHUS, 2010a, 2010b), except in unionoids (ROE, SIMONS, & HARTFIELD, 1997) (see sections on Early Development of the Ligament, p. 28–30, and Early Development of Hinge Teeth, p. 30–50). Amorphous calcium carbonate does not seem to play an important role in the biomineralization of the postlarval shell (WEISS & others, 2002). Mineral phases are almost exclusively aragonitic or calcitic, with vaterite being extremely rare in bivalves (SPANN, HARPER, & ALDRIGE, 2010) and presently unknown from nepioconchs. Within the periostracum, mineralization is limited to aragonite and certain calcium phosphatic minerals (CARTER, 1990).

Nepioconchs may possess a continuous granular or prismatic outer shell layer. This outer shell layer often develops noncommarginal, most typically antimarginal—oriented more or less perpendicular to successive shell margins (CARTER & others, 2012)—microsculptures (e.g., many pteriomorphs). Where this layer is missing, sculptures are commonly defined by fine to crowded commarginal growth increments and a lack of radial elements (e.g., many arcoids and heterodonts). The transition toward later growth stages is gradual but better marked, overall, in taxa with a granular to simple prismatic adult outer shell layer. Mesoconch structures are too little known to be considered here.

It seems that the presence or absence of a granular to simple prismatic outer shell layer and related microsculptural patterns of the nepioconch are largely genetically

controlled. This is especially evident in the Pectinidae. Hypotheses involving other controlling factors (e.g., role of the periostracum, crystallographic constraints, and habitat change) are speculative at present.

### INDISTINCT SHELL STAGE BOUNDARIES

Some autobranchs show unusual shell topologies and often ill-defined stage boundaries between P-1 and P-2, and sometimes also between P-2 and nepioconch (see definition of metaconch and cryptoconch, p. 3, herein). The underlying processes are not understood. However, there is sufficient evidence to correlate these growth patterns with extended brooding (HAYAMI & KASE, 1993; MIDDELFART, 2002a; OLIVER & HOLMES, 2004; this study). Because the distinction of shell stages is important for homology hypotheses and for a morphology-based classification, shells with indistinct boundaries (or where a clear boundary could represent either P-1/P-2 or P/N) are presently called cryptoconch rather than prodissoconch or metaconch.

### SHELL ORIENTATION

Oriental terms for the prodissoconch, nepioconch, and mesoconch largely follow the rules for adult shells. The first approximation to the anterior-posterior shell orientation is provided by the mouth-anus body axis (often inferred). The umbo, including the center of shell calcification (cicatrix), and the hinge are dorsal. The length axis of the shell is defined parallel to the straight hinge axis of the prodissoconch-1 (P-1-HA) and the height axis normal to the straight hinge (and length). Consequently, each shell valve can be divided into anterodorsal, anteroventral, posteroventral, and posterodorsal quadrants. These will be later used in shape descriptions and graphic representations (p. 11, herein).

As in adult bivalves, shell and anatomical body axes and planes of the developing larva rarely coincide, except for the sagittal (body) and commissural (shell) planes (where the

shell valves meet). In contrast to the adult animal, the mouth-anus axis may rotate during early ontogeny. Many early workers did not explicitly define a reference line for shell length, whereas other early workers apparently regarded length as synonymous with the largest diameter (LD) across the shell. The corresponding axis is called the major shell axis (MA) herein, but measurements based on this axis are discouraged because the MA typically shifts with respect to the straight hinge line of the prodissoconch, as a result of allometric growth (Fig. 5). Therefore, the straight hinge axis of the P-1 is used as a fixed reference line, as in the length definition discussed previously. In instances where the straight hinge intersects the commissural plane (e.g., larval shells with coiled umbos) or where it is hidden from direct observation (e.g., external shell views), the best visual approximation to that line is used.

### SHELL DIMENSIONS AND RATIOS

Length and height are the shell dimensions most commonly measured. Unless stated otherwise, they apply to metamorphically competent larvae. P-2 dimensions refer to the size of the entire larval shell, including the P-1. Overall, prodissoconch-1 lengths range from ~35  $\mu\text{m}$  to 425  $\mu\text{m}$  or exceptionally 750  $\mu\text{m}$  in autobranchs, and up to 1350  $\mu\text{m}$  in protobranchs.

The smallest prodissoconchs of competent larvae range from ~135  $\mu\text{m}$ , as in *Nuculana trochilia* (DALL, 1898) (LABARBERA, 1974), to 141  $\mu\text{m}$ , as in *Crenella magellanica* LINSE, 2002 (Fig. 6.1–6.2), and both dimensions refer to prodissoconch-1 alone: P-2 is not developed in protobranchs nor, to our knowledge, in the mytilid genus *Crenella* T. BROWN, 1827. Autobranch prodissoconchs with a well-developed P-2 commonly range from ~190  $\mu\text{m}$  (e.g., *Anomia ephippium* LINNAEUS, 1758; LE PENNEC, 1978) to ~500  $\mu\text{m}$ , but some may reach 800–1300  $\mu\text{m}$  in length. About the same range (170–1300  $\mu\text{m}$ ) is found in metaconchs and cryptoconchs but

with dimensions above 500  $\mu\text{m}$  being more common. It should be noted, however, that measurements of larger-sized early ontogenetic shells may be erroneous due to misidentified prodissoconch/nepioconch boundaries. Shell thickness in a bakevelliid P-2 was found to vary between 10–23  $\mu\text{m}$  (MALCHUS, 2004a); other species may be somewhat thinner. There seems to be no available data on the shell thickness of metaconchs and cryptoconchs.

Dimensions of P-1, P-2, and metaconchs or cryptoconchs are sometimes used as characters of taxonomic importance because they may differ considerably among taxa, even between closely related species (OCKELMANN, 1965). However, the most pervasive application of absolute P-1 sizes, and ratios between P-1 and P-2 sizes has been to infer approximate egg sizes (yolk mass) and developmental modes (OCKELMANN, 1965; BERKMAN, WALLER, & ALEXANDER, 1991; see JABLONSKI & LUTZ, 1983, for a review). The present approach does not follow this classic path (see section on Early Ontogenetic Shell Typology, p. 50–59, herein).

Numerous other dimensions or ratios have been proposed to describe larval shell geometry and allometric growth: shell depth or convexity, umbonal length, height and length of the anterodorsal and posterodorsal shell regions (shoulders), straight hinge length, and the shell size at which the umbo appears (LOOSANOFF, DAVIS, & CHANLEY, 1966; CHANLEY & VAN ENGEL, 1969; LABARBERA & CHANLEY, 1970; CHANLEY & ANDREWS, 1971; LABARBERA, 1974; CHANLEY & CHANLEY, 1980; HU & others, 1993; MALCHUS, 1995, 1999). Although some of these additional measurements and geometric descriptors show taxon-specific characters, none of them has become widely used.

### GRAPHIC AND NUMERICAL REPRESENTATIONS OF SHELL SHAPE

Shell shape is described in terms of outline and profile. Outline refers to the two-dimensional projection of the shell border on a plane parallel to the commissure. Profile

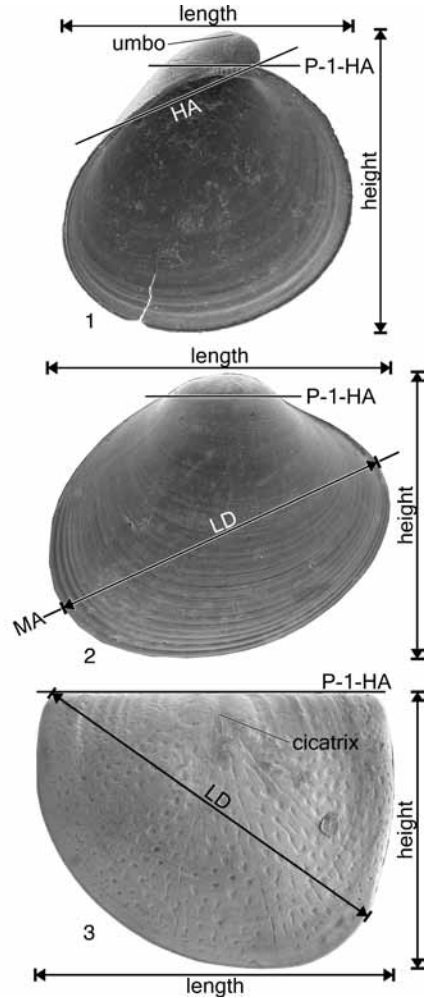


FIG. 5. Axes and dimensions used in descriptions of bivalve shell stages; length and height are measured parallel and normal to hinge axis of prodissoconch-1 (*P-1-HA*), respectively; 1, bakevelliid species morphotype M1, Jurassic (MALCHUS, 2004a), in which largest dimension (*LD*) of shell along a straight line (major shell axis, *MA*) coincides with height; *P-1* hinge axis (*P-1-HA*) is not equal to hinge axis (*HA*) of entire shell (drawn from most posterior to most anterior teeth); 2, *Musculus subpictus* (CANTRAINED, 1835); 3, *Philobrya wandelensis* LAMY, 1906 (new).

is defined herein as the contour of the shell perpendicular to the outline, as seen from the dorsum (Fig. 6).

Outline drawings or equivalent micrographs are useful for capturing and comparing

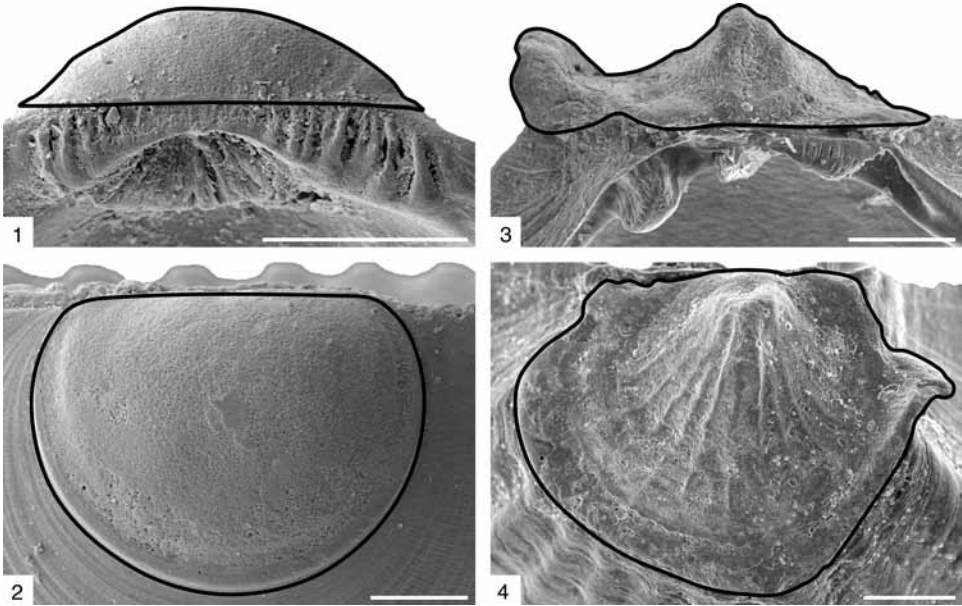


FIG. 6. Profiles (1, 3) and outlines (2, 4) of early ontogenetic shells; 1–2, *Crenella magellanica* LINSE, 2002, left valve of prodissoconch-1, scale bars, 100  $\mu\text{m}$  (view 1) and 50  $\mu\text{m}$  (view 2) (Malchus & Linse, new); 3–4, *Condylocardia hippopus* (MÖRCH, 1861 in 1859–1861), left valve of cryptoconch; scale bars, 100  $\mu\text{m}$  (new).

the most elementary shape characteristics and growth changes, and to establish identification keys (e.g., JØRGENSEN, 1946; SULLIVAN, 1948; REES, 1950; LOOSANOFF, DAVIS, & CHANLEY, 1966; CHANLEY & ANDREWS, 1971). However, differences are often rather subtle, and the associated drawings and data are generally not uniformly presented, thereby hampering comparisons. These difficulties can be avoided by using standardized outlines (MALCHUS & WARÉN, 2005; contour graphs of MALCHUS, 2006), based on a set of rules (Fig. 7).

To construct a standardized outline, the original image is rotated until the straight hinge is horizontal. The outline is then drawn and a scale bar added. All outlines are based on the left valve exterior. Left valves of inequivalve bivalves tend to be larger than right valves (e.g., oysters, anomiids), and using the exterior view (with the commissure facing down on a flat surface) guarantees a proper orthogonal view unless the commissure plane is warped (as in many oysters). In equivalve shells, drawing the outline from the left valve

exterior is equivalent to drawing it from the right valve interior—it is also equivalent to the mirror images of the two remaining perspectives. To complete the figure, the outline is first inscribed into a rectangle that will serve only as reference; then, a circle is drawn centered relative to the rectangle and circumscribing the shell outline (there is generally only one contact point); finally, the reference rectangle is removed from the drawing. The figure can be divided into quadrants or octants for easier description. EVSEEV and KOLOKUTHINA (2008) developed a similar representation called a cyclogram (see also EVSEEV, KOLOKUTHINA, & KULIKOVA, 2011), with a circle adapted to the inner shell margin. However, the authors did not provide any rules for standardization, and the method seems to involve more steps than standardized outlines (MALCHUS, 2006).

For profile drawings (prodissoconch, metaconch, or cryptoconch), the shell is tilted to provide a dorsal view. The positioning may be only approximate. Profiles have rarely been shown or described, but they

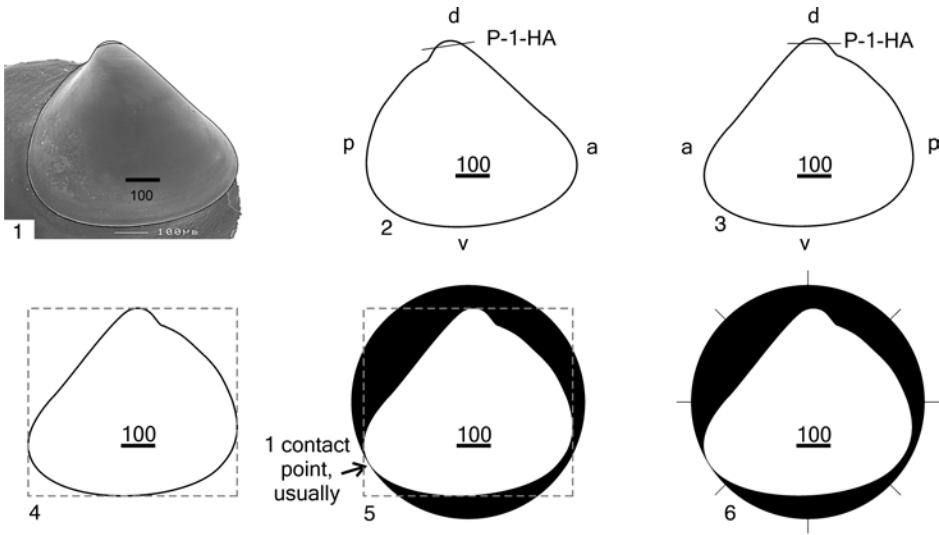


FIG. 7. Steps in preparation of a standardized outline of a right valve of a pinnid; 1, original image with scale bar; 2, outline and estimated position of hinge axis are drawn and scale bar is retained; 3, outline is mirrored horizontally to mimic outline of left valve and rotated until hinge axis is horizontal; 4, outline is inscribed into a rectangle; 5, circle centered with rectangle and circumscribing outline is added to figure; there is usually only one point of contact between circle and outline; 6, standardized outline is finished by removing rectangle and dividing circle into octants; *a*, anterior; *d*, dorsal; *p*, posterior; *P-1-HA*, hinge axis of prodissoconch-1; *v*, ventral (new).

can provide useful additional information regarding morphology, convexity, and growth symmetry. In this chapter, profiles are part of the morphological definition of shell types (see discussion of Early Ontogenetic Shell Typology, p. 50–59, herein).

Other simple graphic or statistical methods include length versus height plots of larval growth series (e.g., LOOSANOFF, DAVIS, & CHANLEY, 1966; reprocessed by MALCHUS, 1999) and three-dimensional graphic representations based on shell length, height, and width (CHANLEY & VAN ENGEL, 1969). However, both methods require large datasets, which are rarely available; in addition, the measurements are time consuming, and the graphs are not easily compared. Modern approaches would certainly apply the much more versatile and powerful techniques of multivariate statistics and geometric morphometrics (e.g., ZELDITCH & others, 2004; MACLEOD, 2007, 2008). HENDRIKS, DUREN, and HERMAN (2005) developed a computer-aided automated identification tool for bivalve larvae that includes the

determination of eigenvector and eigenshape values. Otherwise, these methods have not yet been applied to bivalve larval shells.

## SHELL STAGE CHARACTERS

### PRODISSOCONCH-1

#### Shell Shape

Apparently all bivalves have an equivalve but not always equilateral prodissoconch-1 (see section on Early Ontogenetic Shell Typology, p. 50–59, herein). Outlines may be almost round, indistinct, or broadly rounded (CHANLEY & ANDREWS, 1971) to ellipsoidal or D-shaped in autobranchs, due to their straight hinge line (Fig. 4.1, Fig. 8–9). D-shaped and ellipsoidal P-1 shells are typically longer than high.

Umbonate shells of autobranchs usually possess an ellipsoidal P-1 ( $L > H$ ). In contrast, non-umbonate taxa with the P-2 either narrow or lacking (some Limidae, Limopsidae, Crenellinae, and Thyasiridae) tend to have a roundish or weakly asymmetrical D-shaped P-1 (Fig. 9). Some taxa (e.g., some

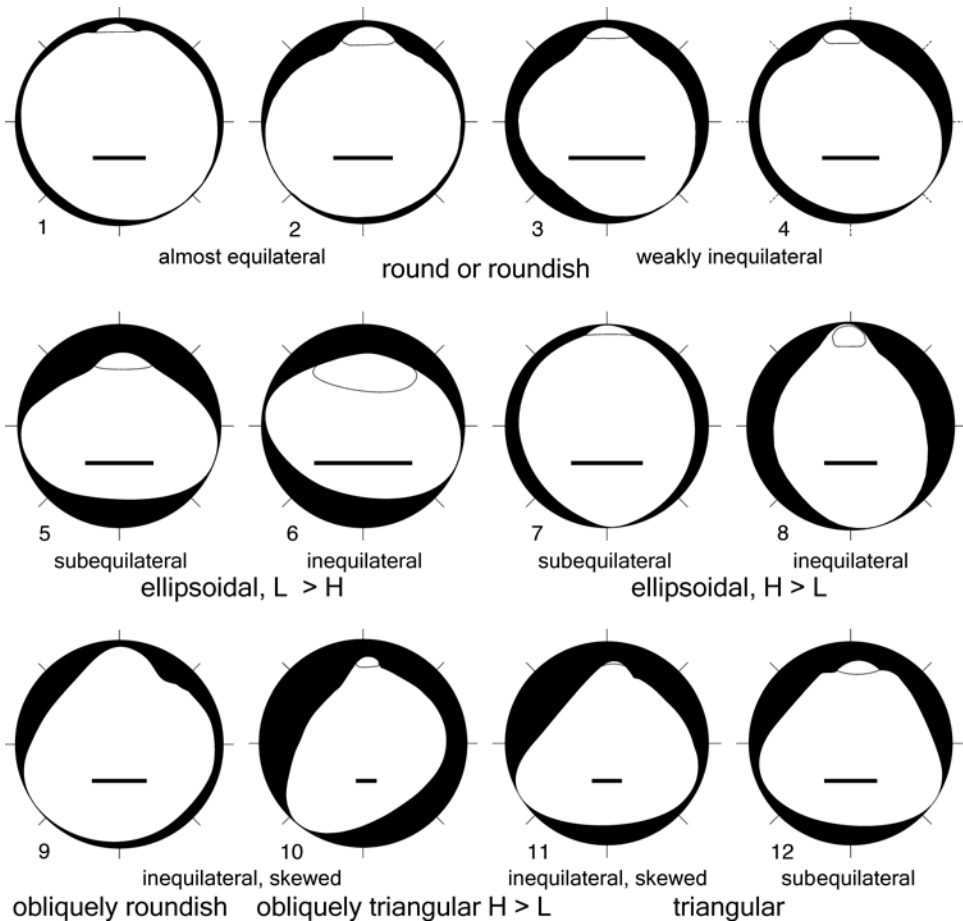


FIG. 8. Contours of umbonate prodissoconchs, representing views of left valve exterior, with boundary of P-1 indicated by incised line; 1, morphotype M9 (?pectinoid, Jurassic), MALCHUS (2004a); 2, pycnodontid; 3, *Anomia* LINNAEUS, 1758; 4, xylophagine; 5, *Grammatodon* MEEK & HAYDEN, 1860 (Jurassic); 6, *Sriarcar lactea* (LINNAEUS, 1758); 7, *Teredo navalis* LINNAEUS, 1758; 8, morphotype M8 ?*Kobayashites* HAYAMI, 1959 (bakevelliid, Jurassic), MALCHUS (2004a); 9, *Cubitosrea sellaeformis* (CONRAD, 1832 in 1832–1835); 10, morphotype M4 (?bakevelliid, ?pinnid; Jurassic), MALCHUS (2004a); 11, pinnid (?*Atrina* GRAY, 1842); 12, *Limaria loscombi* (G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834); all scale bars, 100  $\mu$ m (new).

Limopsidae) develop a tiny bump in the center of the cicatrix, which may be surrounded by a weak, moatlike depression (MALCHUS & WARÉN, 2005). Others possess distinctive profiles and sculptures (see Shell Type 3B, 3C in section on Early Ontogenetic Shell Typology, p. 56–58, herein).

Among protobranchs, roundish larval shell outlines are found in nuculids; ellipsoidal larval shells seem to be more common in nuculanids and solemyids. The profiles are usually weakly to moderately

convex and may be almost equilateral or variably wedge-shaped. Wedge-shaped profiles are apparently always steeper on the posterior flank, which allows one to discriminate left from right larval valves. The central area is often weakly dented. Deeply depressed cicatrix areas are rare; they may be bordered by a horseshoe-like ridge and superficially approach some autobranch larval shell morphologies (see discussion of Shell Type 3C, p. 56–58 herein).

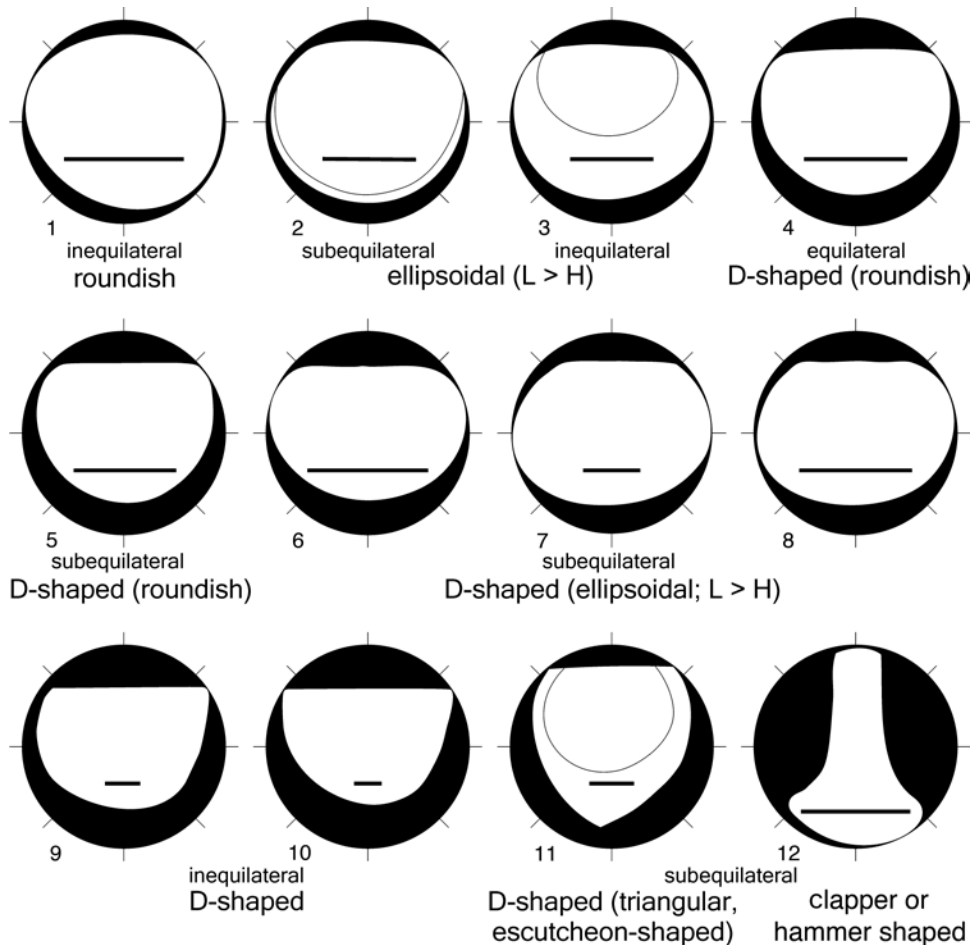


FIG. 9. Contours of non-umbonate prodissoconchs, representing views of left valve exterior, with boundary of P-1 indicated by incised line; 1, *Austronucula perminima* (MONTEROSATO, 1875a) (= *Nucula recondita* GOFAS & SALAS, 1996); 2, *Cyprogenia stegaria* (RAFINESQUE, 1820); 3, *Glycymeris violacescens* (LAMARCK, 1819 in 1818–1822); 4, *Crenella magellanica* LINSE, 2002; 5, *Limopsis cristata* JEFFREYS, 1876; 6, *Saccella commutata* (PHILIPPI, 1844); 7, *Lasaea colmani* Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999; 8, *Nuculana pella* (LINNAEUS, 1758); 9, *Philobrya wandelensis* LAMY, 1906; 10, *Philobrya brattstromi* SOOT-RYEN, 1957; 11, *Anodonta anatina* (LINNAEUS, 1758); 12, *Potamilus obiensis* (RAFINESQUE, 1820); all scale bars, 100  $\mu\text{m}$  (new; outlines of views 2, 11, 12, adapted from Hoggarth, 1999).

### Sculpture and Fine Structure

The cicatrix is usually flattened or slightly dented, sometimes with a weak, dorsal-ventral incision and small, roundish pits (Fig. 4.3; punctate-stellate zone of CARRIKER & PALMER, 1979). This sculpture is covered by the periostracum, which may hide the underlying shell surface, and which may have its own sculptural features (Fig. 10). Viewed from the outer surface, the microstructure appears to

consist of randomly oriented, short, needle-like crystals.

Beyond the cicatrix, the P-1 may have an outer shell crust with antimarginally aligned crystals and a finely cross-hatched microstructure below or substituting that layer. The latter microstructure gradually changing into a more regular pattern of longer, antimarginally oriented crystal needles (Fig. 4.2, Fig. 4.4). These features may be poorly visible through the periostracum. Some of

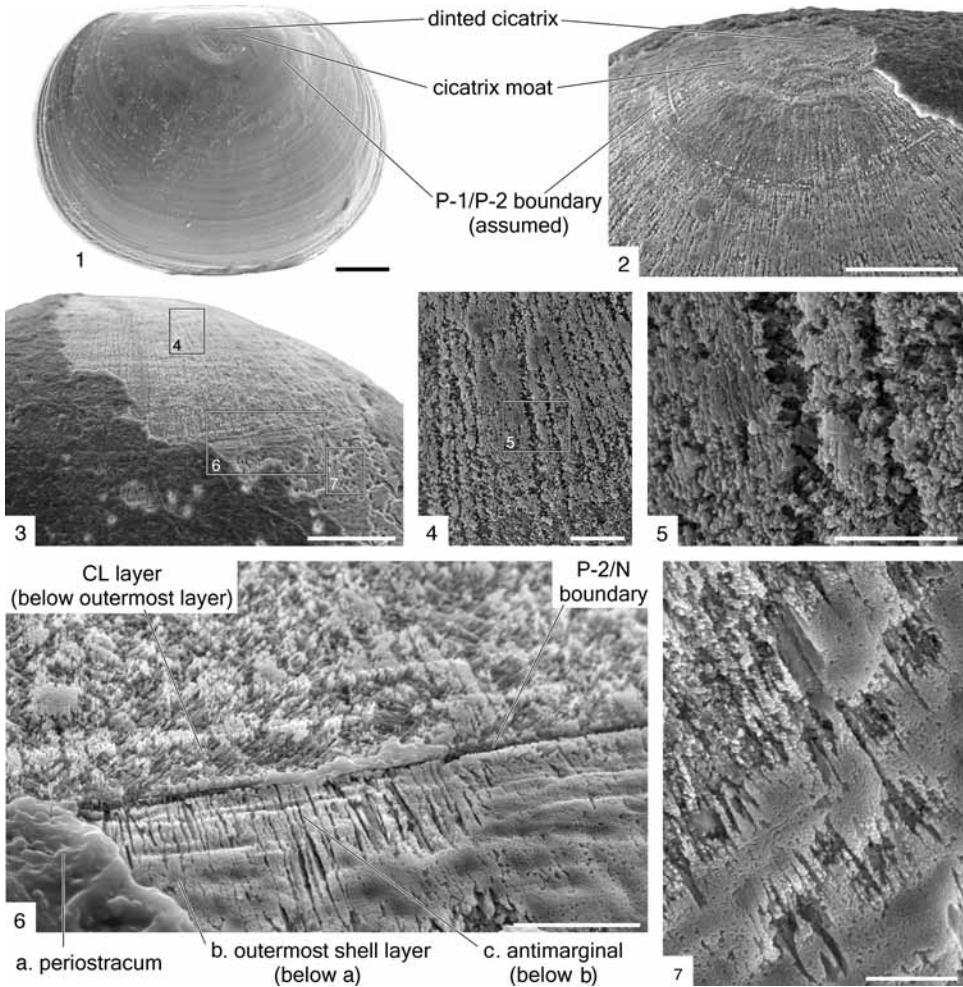


FIG. 10. Microstructure of prodissoconch and nepioconch of *Lasaea colmani* Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999; 1, general view of prodissoconch of an untreated specimen, scale bar, 50  $\mu\text{m}$ ; 2, prodissoconchs-1 and 2 of a bleached specimen, scale bar, 50  $\mu\text{m}$ ; 3, prodissoconch-2 and nepioconch (*N*) of a bleached specimen, scale bar, 50  $\mu\text{m}$ ; 4, inset of area delimited by corresponding rectangle in view 3, showing microstructure of outer shell layer, scale bar, 10  $\mu\text{m}$ ; 5, inset of delimited area in view 4, showing details of antimarginally aligned crystals of outermost shell layer, scale bar, 5  $\mu\text{m}$ ; 6, inset of area delimited by corresponding rectangle in view 3, showing a crossed lamellar layer of P-2 and three different layers of N, scale bar, 10  $\mu\text{m}$ ; 7, inset of the area delimited by corresponding rectangle in view 3, showing relationship between outermost and antimarginal layers of nepioconch, scale bar, 5  $\mu\text{m}$  (new).

the antimarginal crystal needles may project slightly, forming fine antimarginal threads, riblets, or ribs on the shell surface (especially in metaconchs and cryptoconchs). Whether the so-called needles are linearly aligned granular nano-crystals or composite prisms is presently unclear. Note that this description deviates somewhat from CARRIKER and

PALMER (1979, p. 108) and may reflect variations in shell development in different taxa.

Both punctate-stellate and antimarginal zones may show commarginal growth lines that become more pronounced toward the P-1 margin (Fig. 4.2–4.3). Otherwise, the surface of the P-1 is often densely covered by polygonal or angular pits. These pits are



not muscle traces. In marine species, they are restricted to the outermost shell layer and seem to be intimately related to the overlying periostracum and may disappear if the periostracum is eroded. The pits in *Margaritifera auricularia* (SPENGLER, 1793), and probably other unionids, are actually depressions between polyfacetic crystal cones (Fig. 11.2). These are less well developed in the P-1 of *Potomida littoralis* (CUVIER, 1798). After excystment, the P-1 of the latter species becomes covered by a dense pattern of pustules made of irregularly shaped aggregates of nano-crystals, which apparently seal off the larval shell tubules (Fig. 11.3). Hence, pustular or pitted structures of the P-1 in different bivalve groups differ in origin and should not necessarily be treated as homologous.

The prodissoconch (P-1) of protobranchs may also have a weak cicatrix depression. However, muscle traces, commarginal growth lines, and antimarginal elements have not been described in this group. Notwithstanding, protobranchs develop a wealth of surface sculptures at this stage, ranging from pits similar to marine autobranchs (especially in nuculids) to polygonal meshlike or irregularly commarginal corrugations (as in nuculanids, Fig. 12; BENAÏM & ABSALÃO, 2011, in *Tindariopsis* VERRILL & BUSH, 1897).

## PRODISSOCONCH-2

### Shell Shape

Outlines of autobranch prodissoconchs with a distinct P-2 range from round to ellipsoidal or triangular and also from symmetrical to strongly inequilateral. Shells with a small P-1, normally below 145  $\mu\text{m}$ , and a larger P-2 (P-1/P-2 ratio below 0.5) are typically umbonate, with the shell apex projecting beyond the straight hinge (Fig. 1.1–1.2, Fig. 8, Fig. 13). If growth is orthogyrate or nongyrate, such umbonate shells are termed knobby; if the apex and umbo are deflected anteriorly or posteriorly, they are termed skewed (Fig. 8.9–8.11; CHANLEY & ANDREWS, 1971). P-2 profiles may be uniformly convex, with low to high inflation, or they may be umbonate convex. Skewness is generally weakly

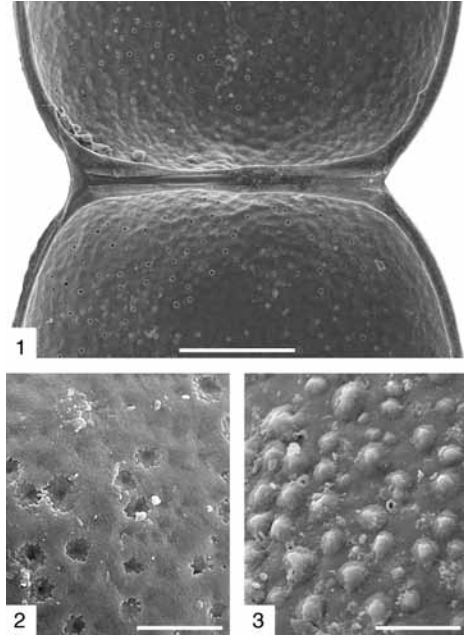


FIG. 11. *Potomida littoralis* (CUVIER, 1798); 1, internal view of glochidial shell, showing tubules, scale bar, 50  $\mu\text{m}$ ; 2, outer surface of P-1 of a freshly released glochidium (before encystment), showing weakly pitted surface and etching traces of tubules, scale bar, 10  $\mu\text{m}$ ; 3, surface of a post-excystment P-1 showing multicrystal aggregates forming small cones on shell, apparently sealing off tubules, scale bar, 10  $\mu\text{m}$  (Malchus & López, new).

expressed in P-2 profiles. Skewed profiles may also derive from nondeflected beaks or apices, depending on a more anterior or posterior position of the beak along the dorsal margin. However, this reflects allometric growth rather than true coiling of the shell.

P-2 shapes may be taxonomically informative. For example, arcoids with a well-developed umbo have symmetrically ellipsoidal P-2 shapes with the length exceeding the height. *Teredo navalis* LINNAEUS, 1758, is symmetrically ellipsoidal with height exceeding length, whereas other umbonate Teredinidae and Xylophaginae are inequilateral-ellipsoidal and globular. Umbonate Limidae have symmetrically triangular P-2s, but Pinnidae have asymmetrically triangular P-2s. Oysters, pteroids, bakevelliids, inoceramids, praeostreids, and

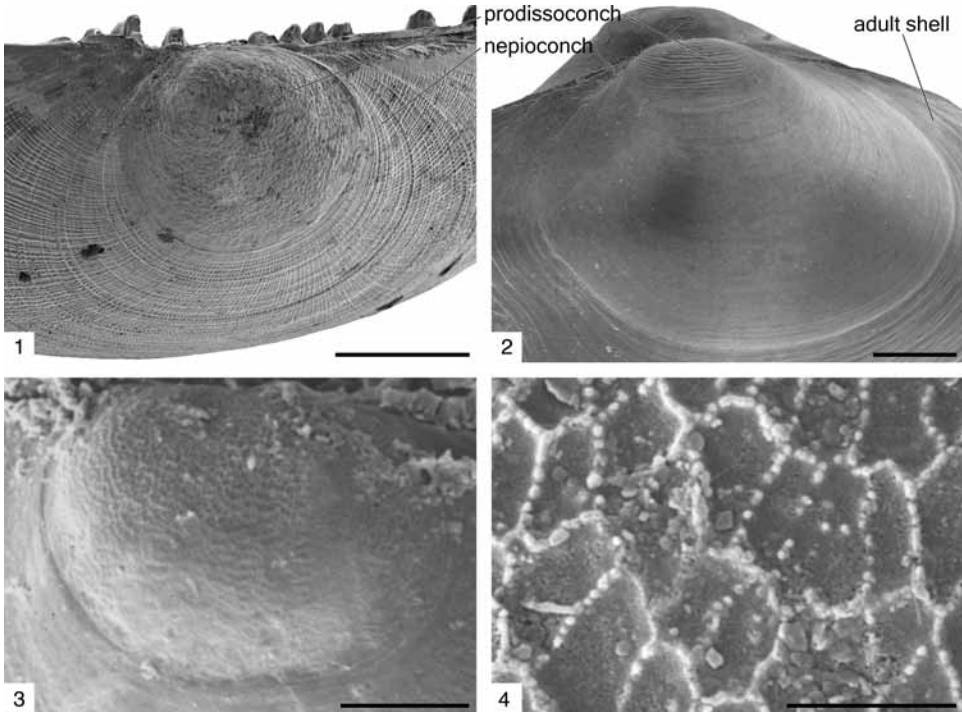


FIG. 12. Examples of surface sculpture in protobranch prodissoconchs; 1, right valve of *Austronucula perminima* (MONTEROSATO, 1875a), showing pitted prodissoconch, scale bar, 100  $\mu$ m; 2, *Nuculana pella* (LINNAEUS, 1758), with corrugated prodissoconch, scale bar, 100  $\mu$ m (new); 3, *Saccella commutata* (PHILIPPI, 1844), showing prodissoconch with meshlike sculpture, scale bar, 50  $\mu$ m; 4, *Saccella commutata*, detail of prodissoconch sculpture, scale bar, 5  $\mu$ m (adapted from La Perna, 2008).

*Butovicella* KRÍŽ, 1965, have opisthogyrate skewed P-2s (KRÍŽ, 1965, 1966; KNIGHT & MORRIS, 1996; MALCHUS, 2000b, 2004a, 2004b). Most Ostreoidea and Anomiidae also have distinctly inequivalve larval shells, with the left valve larger and more convex than the right valve. Prodissoconchs of other cementing bivalves or of ostreoid relatives, such as pterioids and bakevelliids, are (sub)equivalve. In many other umbonate groups, differences are subtler and require further analysis.

Unionid glochidial outlines have received specific names, such as escutcheon-like, if the ventral margin is pointed, or spatulate, if they have a shaftlike dorsal to central part and a broadening ventral border (cf. HOGGARTH, 1999). Profiles appear to be less variable and usually symmetrically convex. However, the

glochidium of *Margaritifera auricularia* (SPENGLER, 1793) becomes much more inflated during encystment (see section on Remodeling of the Larval Shell, p. 27–28, herein).

#### Sculpture and Fine Structure

Well-developed prodissoconchs-2 (P-1/P-2 ratio below 0.75) are usually clearly set off from the P-1 by a narrow gutter and typically bear regularly spaced commarginal growth increments (Fig. 14.1). These increments may develop into washboardlike, regular commarginal growth welts with rounded or steplike crests. They may also become crowded at the end of the stage, giving way to a smooth margin (metamorphic shell lip). The underlying fine structure appears to be essentially antimarginal as in the P-1, best seen when the periostracum and outermost

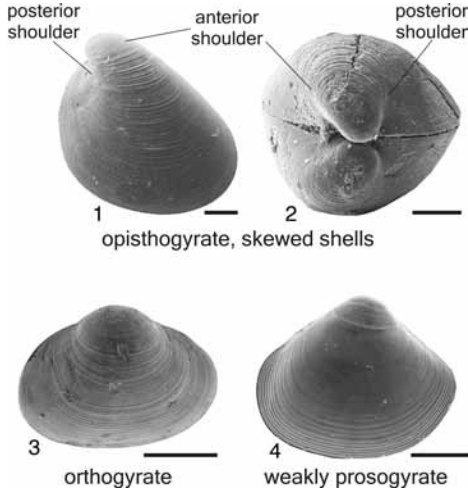


FIG. 13. Examples of early ontogenetic shells with opisthogyrate, orthogyrate, and prosogyrate umbos; 1–2, bakevellid morphotype 3 (Jurassic) (adapted from Malchus, 2004a); 3, *Parallelodon* MEEK & WORTHON, 1866 (Jurassic); 4, *Hiatella arctica* (LINNAEUS, 1767 in 1766–1767); scale bars, 100  $\mu$ m (new).

shell layer are eroded. However, persistence of the punctate-stellate pattern of the P-1 into the P-2 has not been observed (CARRIKER & PALMER, 1979). In shells with a P-1/P-2 ratio above 0.75, the P-2 is often less well defined. In such instances, recognition of the boundaries between P-1, P-2, or the nepioconch may be difficult without knowledge of the time of metamorphosis (Fig. 15–16).

## NEPIOCONCH AND MESOCONCH

### Shell Shape

Nepioconch and mesoconch outlines and profiles have received very little attention. Nepioconch, and thus also mesoconch, growth parameters seem largely decoupled from those of previous stages. Hence, prodissoconch allometric and coiling tendencies may continue, stop, or even invert in the nepioconch, which may lead to opposed coiling directions in the two stages (see section on Opisthogyrate Umbos, p. 26, herein).

### Sculpture and Fine Structure

The prodissoconch-nepioconch boundary is well marked by a commarginal gutter, except

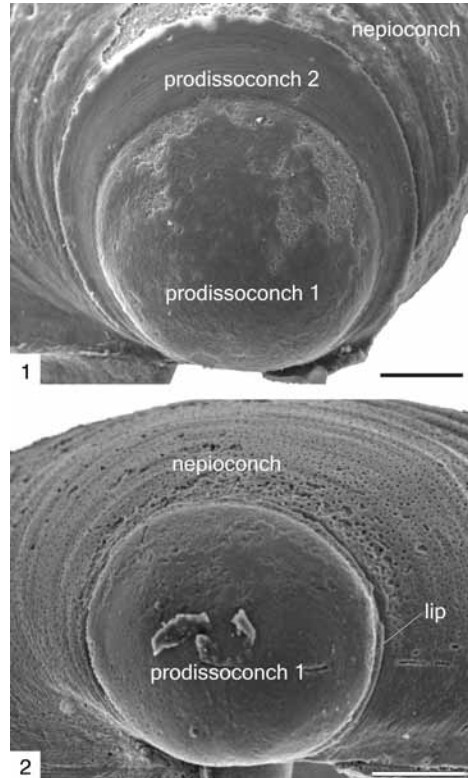


FIG. 14. Examples of autobranch larval shells with and without a prodossoconch-2; 1, right valve of *Parvithracia suteri* FINLAY, 1927, with clear boundaries between prodossoconch-1, prodossoconch-2, and nepioconch, scale bar, 40  $\mu$ m; 2, right valve of *Spheniopsis frank-bernardi* COAN, 1990, with P-2 missing, scale bar, 50  $\mu$ m (new).

where a metamorphic shell lip is present. The lip, which is only a few microns wide, cannot always be clearly attributed to either stage. Beyond it, the shell may be smooth, or it may show commarginal, prismatic, antimarginal, oblique, or reticulate patterns.

Commarginal features are rather variable and may be described as crowded, regularly spaced, sharp-crested, or slightly scaly (e.g., arcids, limopsids, corbulids, *Callocardia* ADAMS, 1864, heterodonts in general) (herein; see also WRIGHLEY, 1946). Densely distributed, continuous antimarginal threads are the most common element found in numerous nuculid Protobranchia,

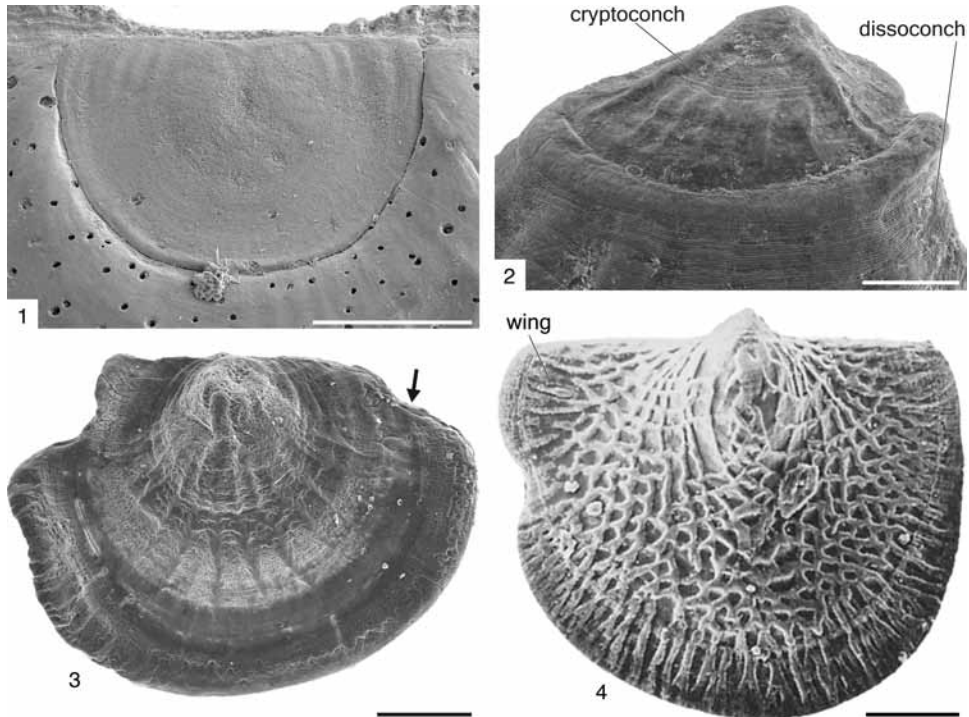


FIG. 15. Cryptoconchs and metaconchs; 1, *Adacnarca* sp. PELSENEER, 1903, with a cryptoconch incrustated in subsequent shell, scale bar, 100  $\mu$ m (new); 2, *Condylocardia digueti* LAMY, 1917, left valve showing cryptoconch (metaconch) with a conus, scale bar, 100  $\mu$ m (new); 3, *C. hippopus* (MÖRCH, 1861 in 1859–1861), metaconch, showing surface sculpture; arrow indicates approximate boundary between prodissoconch and nepioconch, which are welded in this species, scale bar, 100  $\mu$ m (new); 4, *Cycloclamys incubata* (HAYAMI & KASE, 1993), metaconch, external view of left valve, showing anterodorsal wing with sinus almost reaching presumed boundary between larval and nepionic shell, scale bar, 50  $\mu$ m (adapted from Hayami & Kase, 1993).

crenelline and dacrydiine Mytilidae, and some Neoleptonidae, among others (GOFAS & SALAS, 1996, 2008; SALAS & GOFAS, 1997, 1998). They are less dense and finer in *Limaria loscombi* (G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834) (herein). Oblique sculpture forming zigzag shapes of several kinds is present in most Unionida (e.g., ZIERITZ, SARTORI, & KLUNZINGER, 2013). Inconspicuous nepioconchs with only commarginal growth lines have been described in various species of *Limatula* S. V. WOOD, 1839, and *Limea* BRONN, 1831 (ALLEN, 2004). The nuculanids *Nuculana pella* (LINNAEUS, 1758) and *Saccella commutata* (PHILIPPI, 1844) have comparatively short, thickly nodular, bifurcating strings

arranged antimarginally (herein). Several pectinids, anomiiids, species of the fossil dimyid “*Atreta*” ÉTALLON, 1862, and species of *Pinctada* RÖDING, 1798 (HAYAMI & KASE, 1993; MALCHUS, 2000c), show thinner, and more widely spaced, discontinuous threads. In most instances, these structures delimit the nepioconch stage, but they may continue into the adult shell, as in anomiiids and *Limaria loscombi* (G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834). *Dreissena bugensis* ANDRUSSOW, 1897, is exceptional in that it develops continuous antimarginal threads on the advanced P-2 stage (cf. ZARDUS & MARTEL, 2006, fig. 15.14c–d).

Reticulate-angular or diversely pitted and gashed surfaces, typically with antimarginal

orientation, are especially well developed in Pectinidae, and several types may grade into each other (WALLER, 1991, 1993; PEÑA & others, 1998; MALCHUS, 2000c). These features are restricted to the left valve, the right valve being simple prismatic and smooth-surfaced at this stage. Other taxa may show a simple prismatic outer shell layer in both valves at this stage, but the simple prisms may later disappear on the left valve (e.g., in oysters).

The end of the nepioconch stage may be marked by effacement, addition (e.g., radial ribs), modulation (e.g., thickness of commarginals), or substitution of sculpture or microstructure. Ill-defined boundaries, due to gradual transitions, appear to be rather common in porcelaneous-shelled taxa with smooth or only commarginal nepioconch sculptures (e.g., arcoids, heterodonts). Well-demarcated transitions seem to be typical of taxa in which the nepioconch has a continuous aragonitic or calcitic homogeneous/prismatic outer shell layer (e.g., protobranchs, many pteriomorphs). In *Saccella commutata* (PHILIPPI, 1844), the end of the nepioconch stage is additionally marked by the onset of a minute spike-like ornament of the adult shell. Similar ornaments are rather frequent, e.g., in Mytilidae, Cardioidea, Anomalodesmata, and Gastrochaenidae (CARTER & ALLER, 1975; SCHNEIDER & CARTER, 2001), but their onset/offset has rarely been described. Whether the nuculanid structure is of periostracal origin is presently unknown.

Present knowledge of mesoconchs is essentially restricted to the species studied by WRIGHLEY (1946) and a number of Paleozoic taxa described by KRÍZ (see below). In *Callocardia nitidula* (LAMARCK, 1806a in 1802–1806), this shell stage is characterized by the development of a lunula and slight commarginal ridges and furrows, which are delimited by raised rims from the previous and following stages. The mesoconch of *Crassatella* LAMARCK, 1799, is apparently similar to the adult shell of *Astarte* J. SOWERBY, 1816

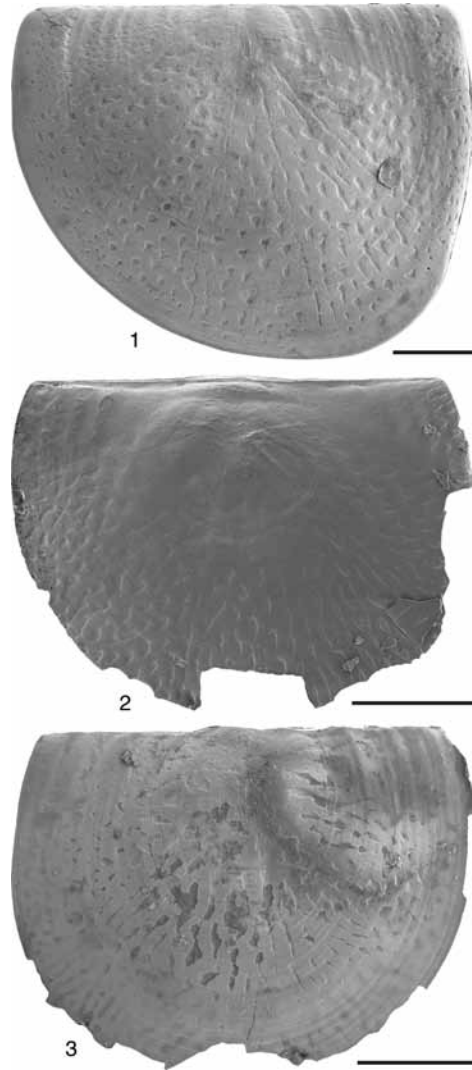


FIG. 16. *Philobrya wandelensis* LAMY, 1906, cryptoconch (or probably metaconch); 1, external surface of fully grown pre-release shell; 2, internal view of cryptoconch of brooded specimen, showing reflection of external sculpture; 3, external view of brooded specimen, in which erosion of periostracum on older portion resulted in larger blotches where underlying shell layer can be seen; scale bars, 100  $\mu$ m (new).

in 1812–1846. In *Plicatula filamentosa* CONRAD, 1833 in 1832–1835, this stage shows small, nodular radial ridges that are first supplemented by coarse ribs and then fade out. The nepioconch of this species

is said to be smooth (WRIGHLEY, 1946, fig. 23–24).

Silurian to Devonian Praeostreinae (Vlastidae) and Silurian Slavidae and Cardiolididae exhibit three to five postlarval shell stages (KŘÍŽ, 1966, 1979, 1985, 1996a, 2007), one of which is, by definition, the mesoconch. In general, one can observe several, more or less prominent changes in sculpture (smooth, commarginal, or radial) bounded by marginal gutters or more gradual transitions. Cardiolid stage boundaries are additionally characterized by prominent, steplike changes from a steep to a shallower commissural angle (that is, the angle between commissural plane and outer shell surface; KŘÍŽ, 1979, fig. 16; 2007, fig. 11). However, according to KŘÍŽ (personal communication, 2010), it is impossible to determine which of the three early stages in cardiolid is the mesoconch.

## METACONCH AND CRYPTOCONCH

### Shell Shape

Larval–early postlarval shells with indistinct stage boundaries may be ellipsoidal (e.g., some species of *Lasaea* T. BROWN, 1827, and *Ostrea* LINNAEUS, 1758) or nearly equilateral to distinctly asymmetrically D-shaped (e.g., philobryid arcoids, many condylocardiids, and some gaimardiids). As discussed in more detail below, deviations from this general outline are caused by winglike extensions of the dorsal shell margin (e.g., in the pectinoid *Cycloclamys* FINLAY, 1926, Philobryidae and Condylocardiidae) or an incomplete nepioconch ring (e.g., some *Condylocardia* BERNARD, 1896c).

Profiles of ellipsoidal shells are generally weakly convex; D-shaped shells may be even less convex (but sometimes also slightly wavy), and then appear more appressed to the postlarval shell. In rare cases, prodissoconchs (or cryptoconchs) have been found leveled with the succeeding shell (Fig. 15.1). Many metaconchs and cryptoconchs have steeply inclined or undercut margins with a flat (plateau- or meseta-like) to wavy surface,

or with a conical inflation, the conus, in the area of the cicatrix, which gives the shell a distinct, hatlike appearance. The tip of the conus may be pointed or depressed, leaving one, sometimes two, horseshoe-like walls or a sharper ridge around it. The conus base does not necessarily define the P-1/P-2 boundary [cf. *Cratis* HEDLEY, 1915; *Cosa* FINLAY, 1926; HAYAMI & KASE, 1993; *Cycloclamys incubata* (HAYAMI & KASE, 1993); *Condylocardia digueti* LAMY, 1917; *C. hippopus* (MÖRCH, 1861 in 1859–1861); Fig. 15.2.4]. The outer rim of hatlike early ontogenetic shells typically consists of nepioconch shell commarginally welded to the P-2 (hence, metaconch). It is sometimes a raised thickened brim or a comparatively thin flaring ring, which may be additionally warped upward (Fig. 15.2). This topography is also reflected in the profile. The steep flanks of plateaulike shells probably also represent nepioconch shell; but as long as this remains unproven, these shells are referred to as cryptoconchs. The second shell stage in the Jurassic *Myoconcha crassa* J. SOWERBY, 1824 in 1812–1846, is also a kind of thin flaring rim, which has been termed collar by KAIM and SCHNEIDER (2012). It appears likely that this shell stage represents the early nepioconch and the entire early ontogenetic shell could be another example of metaconch.

### Sculpture and Fine Structure

In general, metaconch and cryptoconch surface features are characterized by the suppression of typical commarginal ridges of the P-2, the enhancement of antimarginal elements, and the development of coarser sculptures. However, these tendencies may be poorly developed, so that the P-1/P-2 boundary and P-2 commarginals may require transmitted light microscopy for differentiation. These shells may also present relatively few antimarginal low-relief ridges (e.g., *Ostrea chilensis* PHILIPPI, 1868, in KÜSTER & KOCH, 1843–1868; *Lasaea subviridis* DALL, 1899; CHANLEY & DINAMANI, 1980, fig. 12; *Ostrea lutaria* HUTTON, 1873; Ó FOIGHIL, 1986, fig. 3–9). Other taxa possess a relatively thick,

microgranular (homogeneous) outer shell layer. This may contain a dense pattern of subdued ridges or threads, or diversely styled pits, grooves, gashes, thicker ridges, and ribs. Most of these features are aligned antimarginally, as in the Condylocardidae and Philobryidae (DELL, 1964, fig. 2; MIDDELFART, 2002a, 2002b). Larger pits and ridges may be traced on the shell interior (Fig. 15–16). A number of species also produce reticulate or similar sculptures: for example, *Cycloclamys* FINLAY, 1926, and *Cyclopecten* A. E. VERRILL, 1897 (Pectinoidea); *Limatula* S. V. WOOD, 1839 (Limidae); *Acar* GRAY, 1857 in 1853–1857; *Bentharca* VERRILL & BUSH, 1898; *Barbatia* GRAY, 1842 (Arcidae) (see HAYAMI & KASE, 1993; LINSE, 2002; MORAN, 2004a; OLIVER & HOLMES, 2004). Conical elevations often possess distinct sculptural characteristics (Fig. 15.2), and the underlying microstructure is antimarginal granular-prismatic.

The periostracum is typically in contact only with the positive sculptural elements, negative structures (e.g., pits and grooves) being covered by, but detached from the periostracal sheet. Where the periostracum is lost, the outer shell layer is easily eroded, leading to enlargement of negative structures as in *Philobrya melea-grina* (BERNARD, 1896c) and *P. wandelensis* LAMY, 1906 (Fig. 16.3). In some taxa, the outer sculpture of the P-2 continues onto the welded nepioconch, as in *Cycloclamys incubata* (HAYAMI & KASE, 1993), which may lead to a poorly defined P-2/N boundary, as in *Condylocardia hippopus* (MÖRCH, 1861 in 1859–1861) and *C. digueti* LAMY, 1917 (Fig. 15). Brimlike nepioconchs in some species of the philobryids *Cosa* and *Cratis* are coarsely beaded (cf. HAYAMI & KASE, 1993).

### SPECIAL FEATURES

This section covers exceptional shell characters that are typical of a single taxon or that appear to have a limited taxonomic distribution. Most of them are exclusive of the prodissoconch-2; others develop in different stages or can be continuous across boundaries, depending on the taxon

(e.g., shell tubules, coiling tendencies). Hinge teeth and ligament development are discussed separately due to their taxonomic and phylogenetic importance.

### INTERLOCKING

Commissural margins of the prodissoconch-2 stage may be differentiated into an outer ridge and inner groove, so that the valve margins interlock in a tongue-in-groove fashion when the shell is closed (WALLER, 1981, p. 47; pill-box arrangement of REES, 1950, p. 89). This feature is often restricted to the dorsal margins on both sides of the hinge. In most oysters, bakevelliids, the pinnid *Atrina* GRAY, 1842, and the anomiid *Anomia* LINNAEUS, 1758, interlocking occurs along the entire commissure, or nearly so (Fig. 17.1). A similar and probably functionally comparable feature is observed in dwarf males of Xylophaginae, though in this instance the groove marks the onset of postlarval shell secretion and it is the nepioconch lining that grows dorsally into an additional inner lamellar ridge. Interlocking shell margins prevent shearing of the valves. They also play a role in the development of heterodont hinge teeth, as discussed below.

### POSTERODORSAL OUTLET AND RELATED FEATURES

In the prodissoconch-2 of bakevelliids and an undetermined species (morphotype M9 of MALCHUS, 2004a), interlocking larval shell margins are posterodorsally interrupted for ~10–20  $\mu\text{m}$  in both valves (Fig. 17.4), a feature termed the posterodorsal outlet by MALCHUS (2004a) (see also “*Catillopecten*” sp. in KIEL, 2006, fig. 15.6). In oysters, the left valve outlet is complemented by a distinct, sinuous recess of the shell margin, termed the posterodorsal notch (WALLER, 1981) or, more commonly, the fasciole (Fig. 17.2; CARRIKER & PALMER, 1979). The posterodorsal notch and its growth track are exclusive to oysters with a distinct P-2 and develop only within that stage (WALLER, 1981; MALCHUS, 1995, 2000b; JOZEFOWICZ & Ó FOIGHIL, 1998, p. 432). Marked

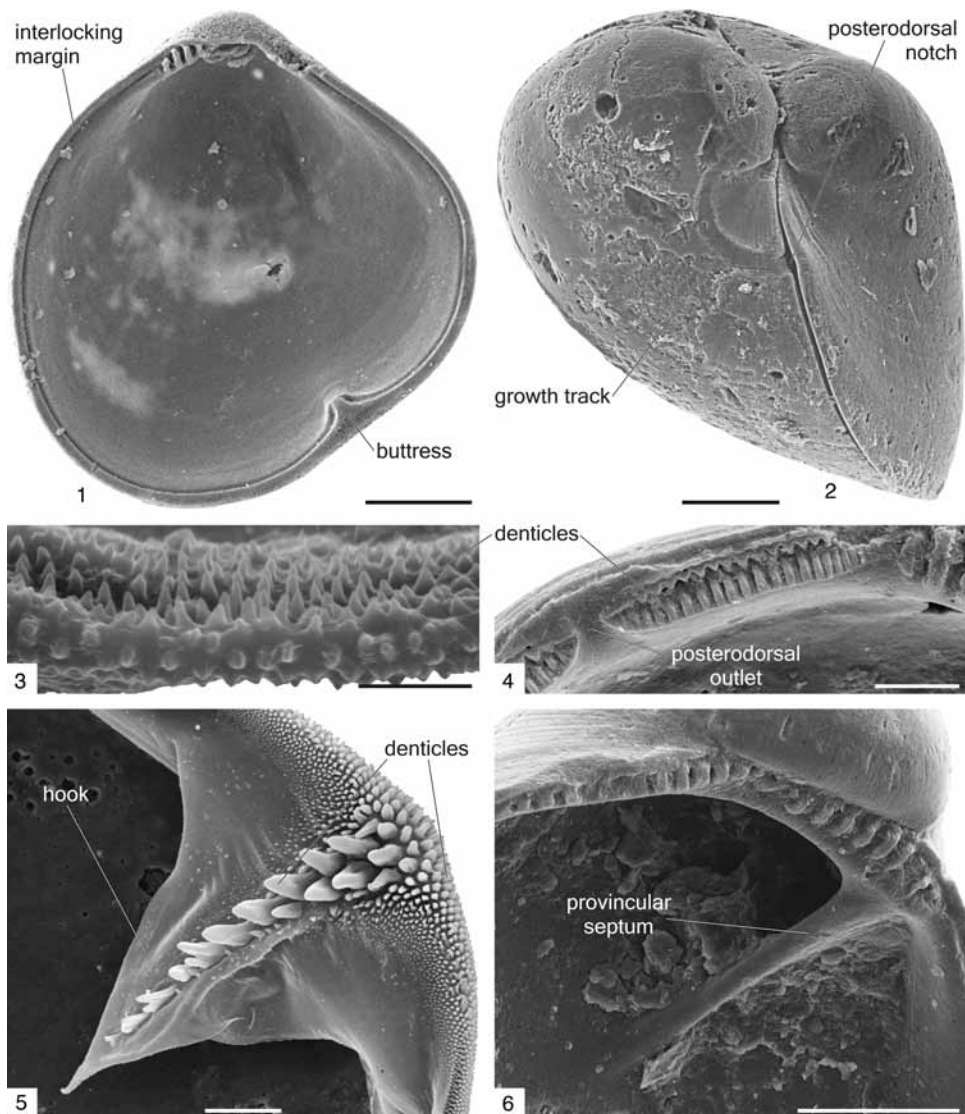


FIG. 17. Examples of special features in early ontogenetic shells; 1, *Anomia* sp., internal view of left valve, scale bar, 50  $\mu$ m (adapted from Malchus, 2004a); 2, *Cubitostrea sellaeformis* (CONRAD, 1832 in 1832–1835), posterodorsal view of shell, scale bar, 50  $\mu$ m (adapted from Malchus, 1995); 3, *Potomida littoralis* (CUVIER, 1798), margin of the prodissoconch, with numerous rows of denticles, scale bar, 5  $\mu$ m (Malchus & López, new); 4, posterodorsal margin of the prodissoconch of bakevellid morphotype 9 (adapted from Malchus, 2004a), scale bar, 20  $\mu$ m; 5, *Anodonta anatina* (LINNAEUS, 1758), ventral margin of glochidial valve, scale bar, 20  $\mu$ m (R. Araujo, new); 6, *Kobayashites* (Jurassic), showing provincular septum, scale bar, 50  $\mu$ m (adapted from Malchus, 2004a).

asymmetry of the notch/outlet seems to be a unique feature of ostreoids, and is apparently related to their inequivalve prodissoconch. In the left and right valves of bakevellids and in the right valves of oysters, the outlet

may cause an almost imperceptible sinuosity of the shell margin, with a barely visible growth trace.

A feature comparable to the growth track of the ostreoid notch was originally



described from some fossil and Recent arcoid genera and termed the posterodorsal ridge by KIEL (2004). It is present in the arcoid *Striarca* CONRAD, 1862 (own data) and also occurs in various pholadids (TURNER, LUTZ, & JABLONSKI, 1985, fig. 24b,c; ZARDUS & MARTEL, 2006, fig. 15.13f). Similarly, the P-2 of some bakevelliids (MALCHUS, 2004a) and of the Recent mytilid *Musculus* RÖDING, 1798, and the nepioconch of *Nuculana pella* LINNAEUS, 1758, show weakly concave growth tracks in comparable positions. Larval and nepionic shells of dwarf males of Xylophaginae possess a faintly posterodorsal outlet with a correspondingly weak shell margin convexity that also seems comparable.

That all these features are homologous cannot be presently ascertained. However, WALLER (1981) demonstrated that the shell notch in *Ostrea edulis* LINNAEUS, 1758, provides a gape for the protrusion of a post-anal ciliated tuft of the veliger larva, possibly aiding in the expulsion of waste products. Ciliated organs in a similar position were also described in veligers of *Tridacna* BRUGUIÈRE, 1797 in BRUGUIÈRE & others, 1791–1827 (LABARBERA, 1974) and in protobranchs (see ZARDUS & MORSE, 1998, p. 240). Hence, there may be a functional link between ciliated organs and these notches, outlets, ridges, and concave growth tracks. In any case, all these features occur in the posterior end of the shell, thus aiding distinction between right and left valves (MALCHUS, 2004a).

#### BUTTRESSES AND RELATED FEATURES

Many Recent anomiiids possess a more-or-less developed sinuous recess and concave growth track on the anteroventral portion of the left valve of the prodissoconch-2. Middle Jurassic *Juranomia* FÜRSICH & WERNER, 1989, is the oldest bivalve known to possess this trait (MALCHUS, 2000a), which is apparently unique to the Anomiidae. At least in some cases, this recess correlates with a distinctive shell buttress on the inner,

anteroventral border of the same valve and with a corresponding recess in the margin of the right valve (cf. LE PENNEC, 1978; MALCHUS, 2000a) (Fig. 17.1). The left valve sinus begins to form approximately at mid-height of the P-2. However, at that stage there is no ridgelike growth track of the buttress on the inner shell surface, suggesting that it develops later than the sinus, near the end of the larval phase. The buttress has only been observed in two specimens; therefore, it is not proven that all individuals with a sinus also possess this structure, and its function is unclear.

Some pholadids develop a similar, tooth-like buttress on the ventral margin of the right valve of the P-2 (WERNER, 1939; JØRGENSEN, 1946; REES, 1950; BOYLE & TURNER, 1976). In *Martesia striata* (LINNAEUS, 1758), the buttress interlocks with two flanking buttresses in the left valve. However, none of these structures seems to generate a sinus or growth track on the inner or outer shell surface (BOYLE & TURNER, 1976, p. 64, fig. 3d–e, 4c–d). According to BOYLE and TURNER (1976), the buttress appears at the onset of larval foot development and becomes overgrown immediately after metamorphosis. Its function is unknown.

#### DENTICLES AND HOOKS

The inner margin of interlocking prodissoconch valves may develop tiny denticles that cannot presently be correlated to the hinge dentition (e.g., Bakevelliidae; Fig. 17.3–17.5). In larval shells of the Jurassic species M9 of MALCHUS (2004a), seemingly unique, interlocking gear-wheel denticles surround the entire commissure except for the hinge and posterodorsal outlet (Fig. 17.4). A similar feature is also developed in the Tertiary “*Catillopecten*” sp., described by KIEL (2006, fig. 15.6). The commissural denticles of this latter taxon are also reminiscent of mytilid larval and early postlarval hinge teeth (see discussion of Hinge Tooth Generation 1b and 1c below, p. 35–38, herein).

Glochidia larvae possess numerous denticles along the anterior, posterior, and ventral shell margins, and many also possess at least one ventral shell hook, armed with spikelike denticles (Fig. 17.3, Fig. 17.5). These shell projections aid the parasitic larvae to attach to their host. Students of the Unionida have developed their own terminology for glochidia marginal denticles (HOGGARTH, 1999). Pustular denticles and absence of hooks, as in some Anodontinae, Lampsilinae, Margaritiferidae, and rarely in *Unio* RETZIUS, 1788, seem to represent the plesiomorphic condition (PEKKARINEN & ENGLUND, 1995a, 1995b; PEKKARINEN & VALOVIRTA, 1996; HOGGARTH, 1999; ARAUJO, TOLEDO, & MACHORDOM, 2009).

#### PROVINCULAR SEPTUM

One Jurassic larval shell type is known to develop a posterior internal shell septum: the larval morphotype M8 of MALCHUS (2004a), possibly the bakevelliid *Kobayashites* HAYAMI, 1959. This structure has been recently termed a provincular septum (TĚMKIN & POJETA, 2010) and is known only from two larval right valves (Fig. 17.6); the corresponding left valve is unknown. A similar structure is present in the early ontogenetic phase of the Recent montacutid genus *Planktomya* SIMROTH, 1896 (GOFAS, 2000). However, the P-2 of this genus is not calcified, and the septum is apparently a postmetamorphic feature. Whether any of these structures is topologically or functionally homologous with the septa or ridges in *Kobayashites*, Cassianellidae, or Lithiotidae is uncertain (TĚMKIN & POJETA, 2010).

#### WINGS, EARS, AND ALAE

Many early ontogenetic shells of marine bivalves as well as glochidial shells show a thickened dorsal margin, anterior, and posterior of the cicatrix, usually set off by a small downward step or flexure toward the main portion of the shell. These sculptural elements are here collectively referred to as wings and have also been called alae in unionids (HOGGARTH, 1999). They are

rectangular (or nearly so) and smooth. Metaconch and cryptoconch wings of marine bivalves are usually elongate triangular and often differ in sculpture from the rest of the shell. One or both wings may protrude slightly beyond the shell disc. The philobryid *Cosa costata* (BERNARD, 1896c) develops two, similar-looking earlike or lobelike extensions at the posterodorsal and posterior shell margins, which appear to be essentially nepioconch features. The anterodorsal wing of the pectinoid *Cyclochlams incubata* (HAYAMI & KASE, 1993) (Fig. 15.4) is a byssus ear, which begins to form during prodissoconch growth, creating a slight inflexion. This inflexion becomes stronger toward the welded nepioconch portion and develops into a typical byssus notch in the right valve, separating the anterodorsal ear from the main body of the shell.

#### OPISTHOGRATE UMBOS

Most umbonate larval shells either lack a clear coiling tendency or are orthogyrate to prosogyrate. Prodissoconchs with opisthocline to opisthogyrate umbos are less common (e.g., the butovicelline *Butovicella* KRÍŽ, 1965; and the Bakevelliidae, Pteriidae, Inoceramidae, and Ostreoidea) (Fig. 13, Fig. 17.2). The influence of coiling on hinge teeth and ligament is discussed later. Coiling tendencies may cease or change their directions at any time after metamorphosis. As a consequence, postlarval coiling directions provide no clues for the direction of larval coiling and vice versa. Even oysters may become orthogyrate, nongyrate, or, rarely, prosogyrate. Similarly, the position of the postlarval umbo along the dorsal shell margin is independent of the larval coiling direction (e.g., opisthogyrate prodissoconchs on anterior umbos of adult shells of bakevelliids and pteriids; MALCHUS, 2004a, pl. 1–2; 2004b, fig. 2, 8). Conversely, tellinid autobranchs and many protobranchs develop opisthocline or opisthogyrate umbos after metamorphosis, which cannot be inferred from their prodissoconchs. These examples

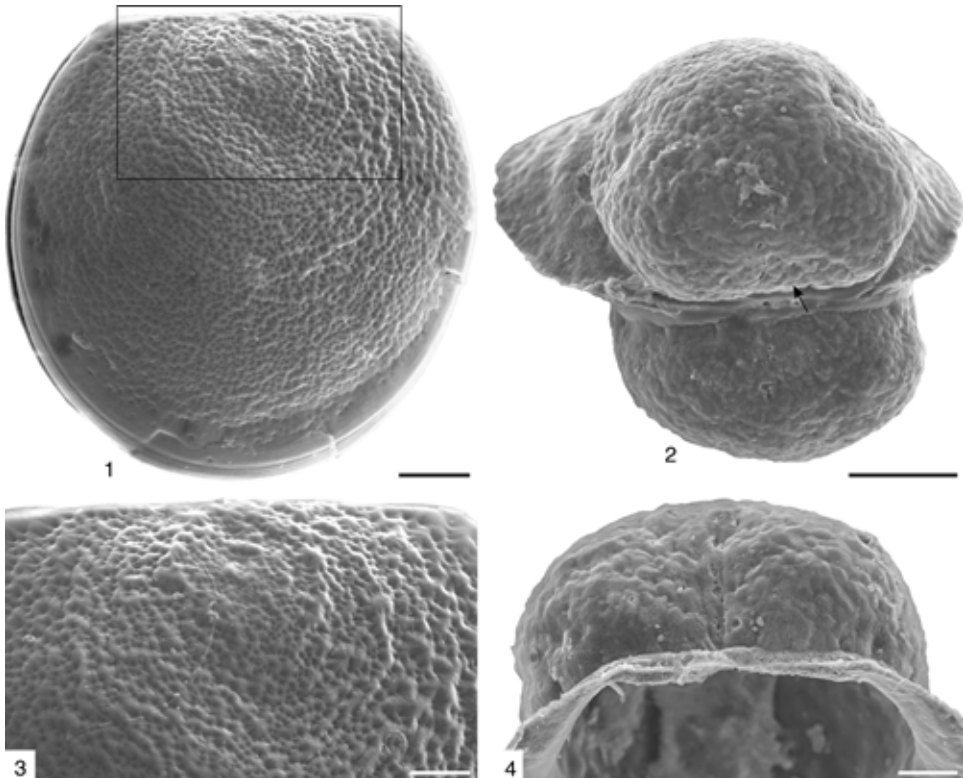


FIG. 18. Remodeling of glochidial shell of *Margaritifera auricularia* (SPENGLER, 1793); 1, shallowly convex shell of a precyst glochidium, scale bar, 20  $\mu\text{m}$ ; 2, shell of excysted individual, with glochidial shell inflated, scale bar, 50  $\mu\text{m}$ ; 3, detail of area delimited by rectangle in view 1, scale bar, 10  $\mu\text{m}$ ; 4, detail of the cicatrix area of view 2 (arrow), showing appearance of a vertical gash, scale bar, 20  $\mu\text{m}$  (Malchus & López, new).

highlight the importance of clearly identifying the coiling direction at each growth stage as well as the postlarval position of the umbo.

#### REMODELING OF THE LARVAL SHELL

True remodeling of the larval shell has hitherto only been observed in the glochidia of *Margaritifera auricularia* (SPENGLER, 1793) (Fig. 18). Although ARAUJO, CÁMARA, and RAMOS (2002) spoke of size increase, their data and present observations on cultured specimens reveal that the glochidium shape and microstructure are actually modified during the parasitic phase. This process transforms a pre-encysted, rather shallowly convex shell

with conical (possibly composite prismatic) crystals of  $\sim 1.5 \mu\text{m}$  width (Fig. 18.1) into a highly inflated, globose, laterally dented shell (Fig. 18.2) with crystal coni about three times larger than before (Fig. 18.3–18.4). In addition, the cicatrix, which was previously hardly visible, now develops a deep, transverse fold. Although significant increase in length and height has also been observed in other species of *Margaritifera* SCHUMACHER, 1816, and in two *Lampsilinae* (see review by BAUER, 1994), current knowledge does not suggest any remodeling in the present sense. Some sculptural modifications are also observed in the glochidia of *Potomida littoralis* (CUVIER, 1798). Although the underlying processes are unknown, these observations raise the

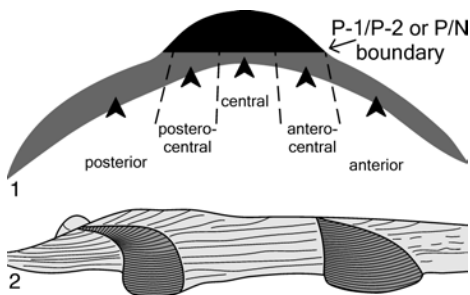


FIG. 19. Developmental aspects of ligaments; 1, diagram of a left valve showing possible origination points for larval (antero- to postero-central) and postlarval ligaments (adapted from Malchus, 2004b); 2, part of hinge of right valve of *Isognomon ephippium* (LINNAEUS, 1758), showing abrupt change in growth direction of first ligament and second ligament positioned posterior to the first (adapted from Jackson, 1890).

question whether similar remodeling could play a role in the development of lateral shell dents and conical inflations in marine bivalves with a reduced P-2, cryptoconch, or metaconch.

### SHELL TUBULES

Tubules in the adult shell are typical of numerous autobranch taxa, including members of the Mytilida, Arcida, Spondylidae, Carditida, Sphaeriidae, Unionidae, and many other groups (see MALCHUS, 2010a, 2010b, for summary and references). Bivalve shell tubules, unlike those of other molluscan groups, are etched into the shell by single-cell extensions of the mantle (REINDL & HASZPRUNAR, 1995). The tubules of most bivalves are an exclusively postlarval feature, although they may also penetrate the larval shell. They begin to form in the nepioconch and are of two types: (1) smooth, 3–7  $\mu\text{m}$  wide, often penetrating the entire shell and inner periostracum layer (e.g., Arcida, Sphaeriidae); or (2) small, often nodular, around 1–2  $\mu\text{m}$  wide, and restricted to the inner and middle shell layers (e.g., Carditida; MALCHUS, 2010a, 2010b). In contrast, unionoid tubules are characteristic of the glochidium and are absent from the post-metamorphic shell (Fig. 11) (ROE, SIMONS,

& HARTFIELD, 1997; HOGGARTH, 1999). Present observations of the margaritifere *Potomida littoralis* (CUVIER, 1798) suggest that its glochidial tubules are sealed off by shell pustules either during encystment or shortly after. Protobranches seem to lack tubules at all growth stages.

### EARLY DEVELOPMENT OF THE LIGAMENT

In most bivalves, the first discernible components of the larval ligament appear during accretion of the prodissoconch-2 and may comprise only a lamellar or also a mineralized sublayer. In autobranchs, this sublayer is apparently exclusively fibrous. There are no data for protobranches. However, some postlarval shells possess granular or granular-fibrous ligaments, which could also exist in their larval or early postlarval shell (e.g., *Neilonella* DALL, 1881; see CARTER, 1990, fig. 7). Development of the mineralized sublayer may be delayed until shortly after metamorphosis, occurring during the early nepioconch (WALLER, 1998; MALCHUS, 2004b). The lamellar sublayer may be external or submarginal, whereas the mineralized portion of the larval ligament appears to be invariably internal; this mineralized portion originates at the anterior, central, or posterior portion of the provinculum in different clades (Fig. 19.1; BERNARD, 1895; WALLER, 1990).

Whereas the position of the ligament's origination appears to be decoupled from other morphogenetic factors, its subsequent growth passively follows the general growth trajectory of the body, being hence correlated with the coiling direction of the shell (MALCHUS, 2004b). In other words, taxa with anteriorly curling beaks (prosoogyrate) have the ligament growing in a predominantly posterior direction (opisthodetic), those with posteriorly curling beaks (opisthogyrate) display an anteriorly elongating ligament (proso-detic), and those without a tangential growth component have the beaks curling directly toward one another (orthogyrate)

and a ligament that grows ventrally (amphidetic). The correlation between coiling and ligament growth direction is most obvious in species that switch coiling direction during ontogeny (e.g., *Isognomon* LIGHTFOOT, 1786), as abrupt shifts in the growth trajectory of the ligament accompany each of the changes (Fig. 19.2) (DOMANESCHI & MARTINS, 2002, fig. 1c–d, 7–8; MALCHUS, 2004b, fig. 4d).

The mineralized sublayer of the larval ligament may continue to grow throughout ontogeny and, together with the lamellar sublayer, may be the sole ligament to form. This type of development has been termed continuous mineralized ligament ontogeny because the adult mineralized ligament is simply a continuation of the first ligament to form: ligament 1 (L1) or larval ligament. Originally, it was called continuous fibrous ligament, as it only referred to Autobranchia (WALLER, 1998); MALCHUS (2004b) distinguished more specifically between mineralized, fibrous ligament (FL) and lamellar ligament (LL). Alternatively, a second, separate, mineralized, fibrous ligamental unit, ligament 2 (L2, or FL2), may form in the early juvenile hinge, in addition to the larval mineralized ligament. In this type of development, termed discontinuous mineralized ligament ontogeny (originally, discontinuous fibrous ligament ontogeny), the adult ligament may comprise only one couplet of mineralized and lamellar layers that was formed subsequent to the first, larval ligament; or it may comprise two or more ligamental units, one of which may be a continuation of the larval ligament. Numerous discontinuous mineralized ligament types are thus formed across the Bivalvia, which are based on variations of two factors: (1) fate of the mineralized larval ligament; and (2) repetitions of the postlarval units. Discontinuous mineralized ligament ontogeny was once considered an exclusive feature of the Pteriomorpha (WALLER, 1998), but it has now been recorded in some Protobranchia and Heteroconchia.

#### FATE OF THE MINERALIZED LARVAL LIGAMENT

Formation of a second ligament unit (L2) in postlarval life commonly correlates with abandonment of the larval ligament (L1), which may then be absorbed or overgrown by subsequent deposition of shell material onto the hinge (Fig. 20.2–20.4). In these instances, typically only one ligamental unit is present in the adult shell. In the absence of data from early juveniles, it may be difficult or impossible to distinguish such a ligament from one produced by continuous ligament ontogeny. However, numerous cases are known in which L1 persists despite the formation of one or more additional ligamental units. Few instances of this mode of development have been studied quantitatively or in great detail, but it seems that if only one additional unit is deposited (L2), that unit grows faster than L1 and becomes the prevalent ligament of the adult hinge (Fig. 21) (TRUEMAN, 1966; SARTORI & BALL, 2009).

In some bivalves the growth trajectories of L1, L2, and subsequently formed units (L3, L4 . . . Ln) overlap, leading to fusion of their fibrous sublayers. The adult ligament then has a morphologically single, but genetically multiple, fibrous sublayer (Fig. 22.1).

#### REPETITION OF POSTLARVAL LIGAMENTAL UNITS

Ligament units formed after the appearance of L2 are very similar to L2 in morphology and mode of growth and are generally regarded as repetitions of the postlarval ligament. This leads to the formation of the duplivincular and multivincular ligament grades discussed elsewhere in this volume. MALCHUS (2004b) explained ligament repetition as a mere continuation of the morphogenetic program leading to formation of L2 in addition to the larval ligament. Repetition of postlarval ligamental units appears to be unique to the Pteriomorpha, as hypothesized by WALLER (1998).

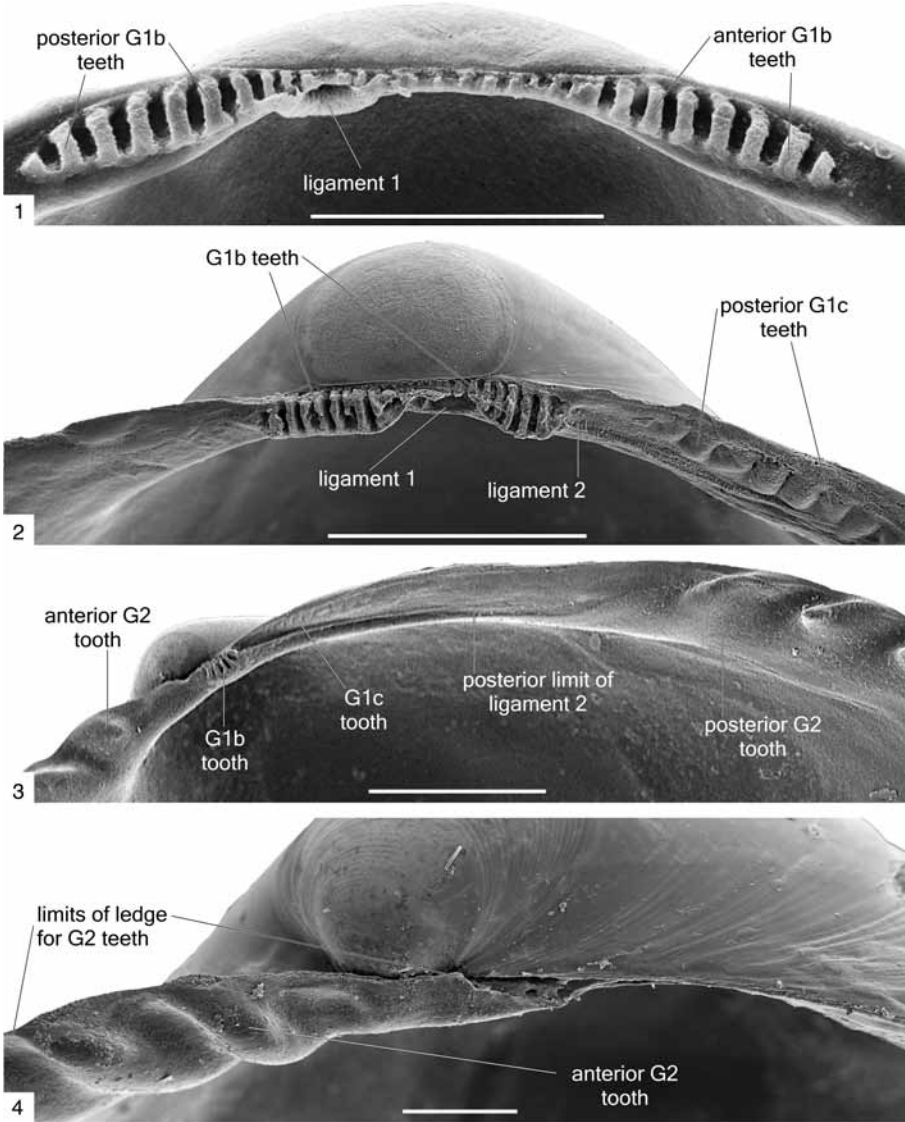


FIG. 20. SEM photos showing stages in development of mytilid hinge teeth and ligament; 1, left valve of early post-larva of *Mytilus galloprovincialis* LAMARCK, 1819 in 1818–1822, scale bar, 50  $\mu$ m (adapted from Malchus, 2000b); 2–4, right valves of postlarva and early juveniles of *Musculus subpictus* (CANTRAINED, 1835); notice that ligament 1 becomes overgrown in this sequence, scale bars: 2, 100  $\mu$ m; 3, 200  $\mu$ m; 4, 100  $\mu$ m (new).

## EARLY DEVELOPMENT OF HINGE TEETH HISTORICAL REVIEW

LACAZE-DUTHIERS (1856, p. 20) was probably the first to recognize the characteristic

toothed hinge of *Mytilus* LINNAEUS, 1758, larvae. Despite this early start, and perhaps excluding the special interest in the post-larval ontogeny of heterodont teeth, systematic studies of the earliest developmental stages of hinges have been relatively rare.

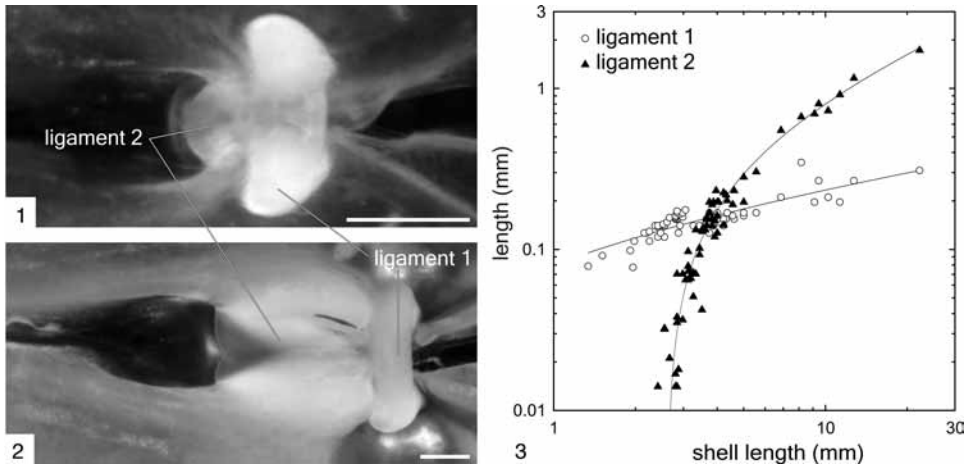


FIG. 21. Allometry of ligaments 1 and 2 in *Thracia phaseolina* (LAMARCK, 1818 in 1818–1822); 1, ventral view of hinge with 4.22 mm shell length, scale bar, 250  $\mu$ m; 2, ventral view of hinge with 10.22 mm shell length, scale bar, 250  $\mu$ m; 3, allometric plot of length of ligaments 1 and 2 on total shell length, showing the much higher rate of growth of ligament 2 (adapted from Sartori & Ball, 2009).

Félix BERNARD's contributions, published between 1895 and 1898, stand out as the most comprehensive reference on this subject, even though his main focus was on early postlarvae (see monographic summary in BERNARD, 1898). REES (1950) is hitherto the only author to develop a suprafamilial classification based on early hinge characters and larval shell shape. ZAKHVATKINA (1959), LE PENNEC (1973, 1978, 1980), LUTZ, GOODSSELL, and others (1982); LUTZ, MANN, and others (1982), JABLONSKI and LUTZ (1983), LUTZ (1985), and SAKAI and SEKIGUCHI (1992) provided additional data for some 60 autobranch species. HU and others (1993) and MALCHUS (1995) reviewed hinge development in living and extinct oysters (see also MALCHUS 2000b, 2004a). MALCHUS and WARÉN (2005) and MALCHUS (2006) provided complementary data on some arcoid families (cf. LUTZ & JABLONSKI, 1978a, fig. 1d; 1981, fig. 1, on a Cretaceous ?mytilid and Recent arcid species, respectively). BERNARD (1896a), GOFAS and SALAS (1996), OCKELMANN and WARÉN (1998), and LA PERNA (2005) give some insights into the early postlarval development of the hinge of protobranches. However, foreshadowed by

BERNARD (1896b), most research on early hinges has concentrated on mytilids (e.g., LE PENNEC & MASSON, 1976; RAMORINO & CAMPOS, 1979; CAMPOS & RAMORINO, 1980; SIDDALL, 1980; RAMORINO & CAMPOS, 1983; KIMURA & SEKIGUCHI, 1994; OCKELMANN, 1995; OZAWA & SEKIGUCHI, 2002; OKUTANI, FUJIKURA, & SASAKI, 2003; OCKELMANN, & DINESEN, 2009), culminating in the detailed studies by EVSEEV and co-workers (EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004a, 2004b, 2005; EVSEEV & KOLOTUKHINA, 2008; SEMENIKHINA, KOLOTUKHINA, & EVSEEV, 2008; EVSEEV, KOLOTUKHINA, & KULIKOVA, 2011).

Mytilids display the most stages of early-hinge development of all bivalves hitherto studied, in a surprisingly complex series. This is not yet understood in all of its details, but it provides the best starting point for a systematic description and understanding of the sequential ontogeny of hinge teeth. The present work distinguishes two main developmental units, termed hinge tooth generations G1 and G2 (MALCHUS & WARÉN, 2005; MALCHUS, 2006). The G1 series is further subdivided into the subseries G1a (larval), G1b, and G1c (postlarval). G2

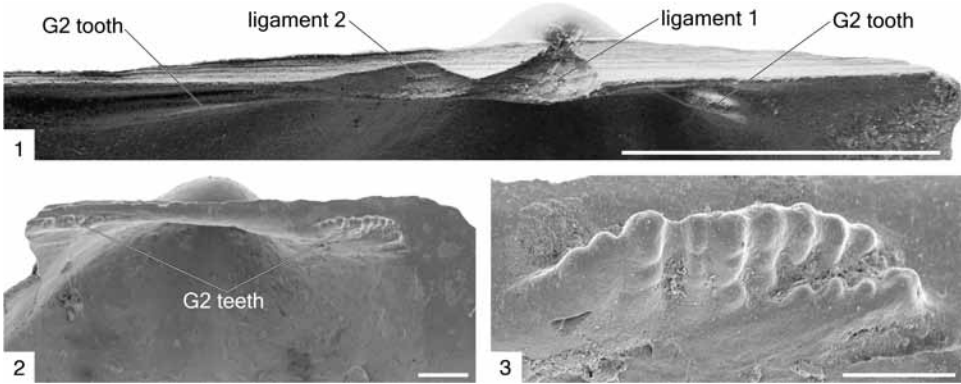


FIG. 22. Generation 2 teeth in Pterioidea and Arcoidea; 1, left valve of *Pteria hirundo* (LINNAEUS, 1758), scale bar, 1 mm; 2, left valve of Jurassic parallelodontid, showing lamellar G2 teeth, scale bar, 100  $\mu$ m; 3, detail of anterior G2 tooth shown in view 2, showing its pustular structure, scale bar, 50  $\mu$ m (new).

series may also have their origin in the larval or postlarval stage but do not form ontogenetic successions like those of G1 (Fig. 20). Potential homologies of hinge teeth grades will be discussed further under the section Homology of Tooth Series (p. 49–50, herein).

### HINGE TOOTH GENERATION 1

Hinge tooth generation 1 (G1) develops during the larval or nepioconch stages (on the provinculum or early postprovinculum, respectively), depending on the mode of development. Well-developed G1 teeth are neotaxodont-like and typically orthomorphodont. They first grow below the straight hinge and later along the posterodorsal and anterodorsal commissural margin, essentially parallel to each other and vertical to the straight hinge and dorsal shell margins.

#### Hinge Tooth Generation 1a

Provincular (G1a) teeth grow during the prodissoconch-2 stage or at the verge of metamorphosis and are restricted to the Autobranchia. Well-formed G1a teeth are sub-equal, quadrangular to rectangular, and normally 2–8  $\mu$ m wide; single teeth may show vertical ridges and grooves.

Mytilid provincular teeth are rather symmetrical. They consist of a medial array

of tiny, poorly developed G1a teeth along the straight hinge, flanked on both sides by a variable number of larger G1a teeth that typically taper distally (Fig. 20.1; primary teeth of SALAS & GOFAS, 1997). This is the central morphogenetic (tooth) field of EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005, p. 1136). During P-2 development, anterior and posterior flanking teeth grow essentially in height; new teeth may be added distally, and medial teeth may become more conspicuous. The fibrous resilifer forms late or even after metamorphosis below the angle formed by the medial and posterior flanking teeth. Crenellinae and at least some Arcuatulinae [e.g., *Brachidontes purpuratus* (LAMARCK, 1819 in 1818–1822)] lack the P-2 stage, and G1a teeth are absent or remain small (–2–3  $\mu$ m; RAMORINO & CAMPOS, 1983, fig. 27; EVSEEV, KOLOTUKHINA, & SEMENIKHINA, 2007, fig. 1c).

In arcooids, the more or less symmetrical provincula are divided by a central to slightly posterior resilifer. Similarly, pectinids and anomiiids have nearly symmetrical hinges but rarely develop more than five G1a teeth flanking a central resilifer, whereas those of pteriooids and pinnids are inequilateral (cf. BERNARD, 1896a, fig. 2, 4; 1896b, fig. 7; BOOTH, 1979a; ROSE & BAKER, 1994). Medial G1a teeth are apparently lacking.



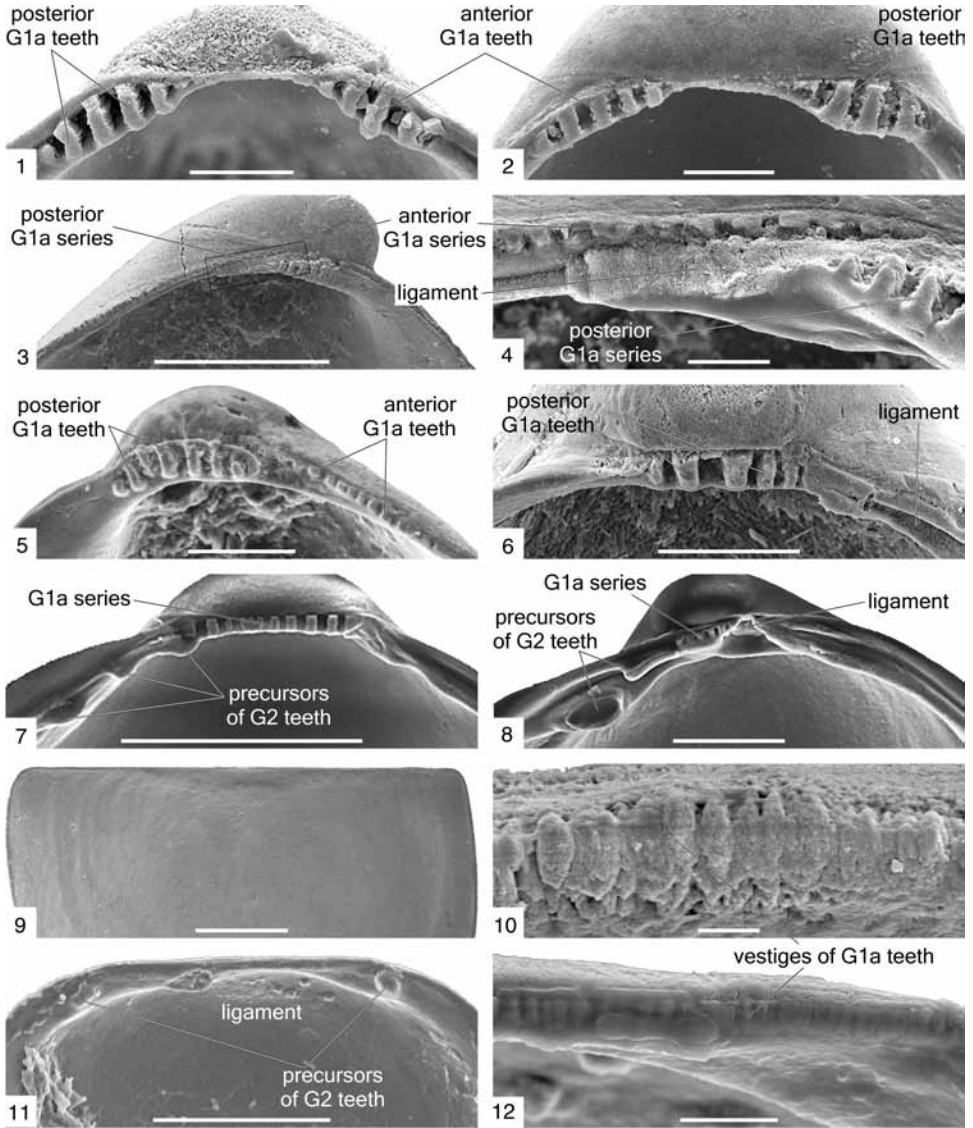


FIG. 23. Provinculum morphology in selected pteriomorphian and heterodont taxa; 1, nearly symmetrical provinculum of an anomiid (LV), scale bar, 20  $\mu$ m; 2, inequilateral provinculum of a pinnid (RV), scale bar, 20  $\mu$ m; 3, partly overlapping anterior and posterior G1a series in a bakevellid (RV) (see hinge of Fig. 5.1), scale bar, 200  $\mu$ m; 4, detail of the area delimited by the rectangle in view 3, scale bar, 20  $\mu$ m; 5, Jurassic exogyrine or liostreine oyster (*Ostreoidea*), with anterior and posterior G1a series (LV), scale bar, 50  $\mu$ m (adapted from Malchus, 2000b); 6, Eocene *Cubiostrea* sp. SACCO, 1897 (*Ostreidae*), lacking an anterior G1a series (LV), scale bar: 50  $\mu$ m (adapted from Malchus, 1995); 7–8, *Alveinus ojanus* (YOKOYAMA, 1927) (*Kelliellidae*), postlarvae (RV), scale bars, 50  $\mu$ m (adapted from Evseev, Semenikhina, & Kolotukhina, 2004c); 9, *Philobrya wandelensis* LAMY, 1906, advanced larval shell extracted from a brooding specimen, scale bar, 100  $\mu$ m; 10, detail of straight hinge in view 9, scale bar, 2  $\mu$ m; 11, *Lasaea colmani* Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999, cryptoconch (probably prodissoconch) extracted from a brooding specimen (LV), scale bar, 100  $\mu$ m; 12, detail of straight hinge of view 11, scale bar, 10  $\mu$ m (new).

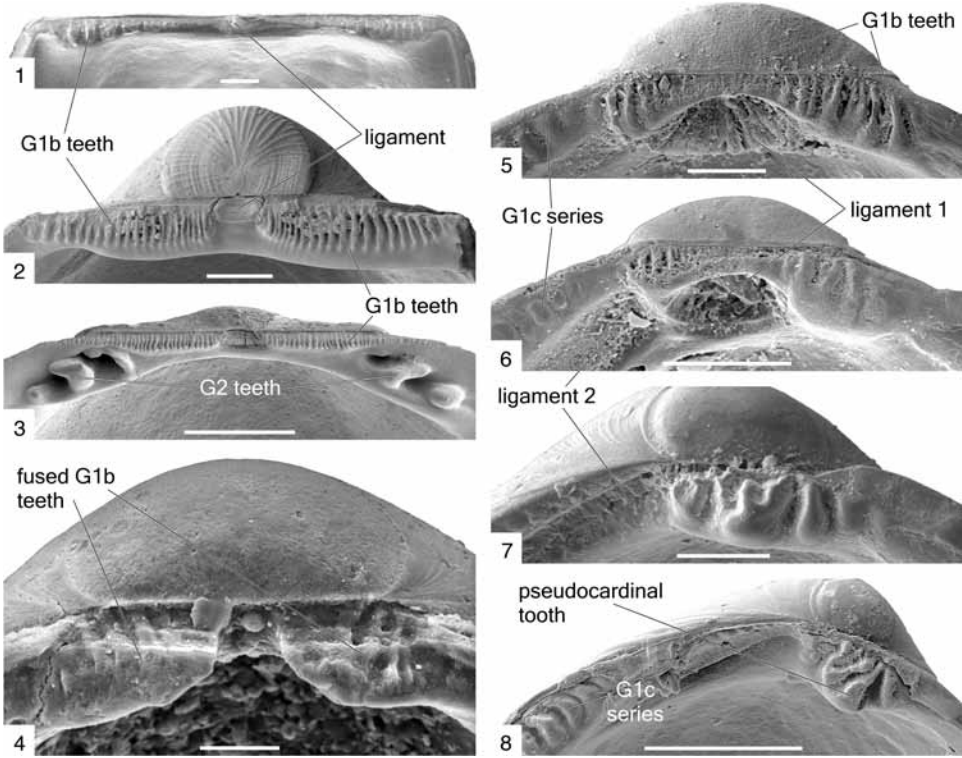


FIG. 24. Early postlarval hinges in selected pteriomorphian taxa; 1–2, *Adacnarca limopsoides* (THIELE, 1912) (Philobryidae); 1, postmetamorphic, prerelease metaconch, scale bar, 50  $\mu\text{m}$ ; 2, early juvenile shell, scale bar, 250  $\mu\text{m}$ ; 3, *Lissarca notorcadensis* MELVILL & STANDEN, 1907 (Philobryidae), early juvenile shell showing both G1b and G2 teeth, scale bar, 300  $\mu\text{m}$ ; 4, *Atreta* species (Dimyidae), showing fusion of G1b teeth, scale bar, 20  $\mu\text{m}$  (adapted from Malchus, 2000c); 5–8, Developmental sequence of *Crenella magellanica* LINSE, 2002, showing different fusion stages of G1b to pseudocardinal teeth, scale bars: 50, 100, 100, and 250  $\mu\text{m}$ , respectively (Malchus & Linse, new).

The strongly opisthogyrate bakevelliids and fossil oysters have numerous G1a teeth. However, the posterior row occupies a position below the straight hinge and is dorsally overlapped by proximal teeth of the anterior row; the larval ligament is sandwiched between the two series and grows anteriorward (Fig. 23.3–23.4).

The anterior row of teeth in oysters was reduced over evolutionary time so that the larval ligament came to lie anterior to the provinculum (cf. demivinculum of BERNARD, 1898; MALCHUS, 2000b). Among living oysters, only the Pycnodontinae (Gryphaeidae) may still show a rudimentary row of a distal, anterior G1a tooth series. In brooding ostreids, the most central subumbonal teeth

are replaced by an elongated, thickened, and sometimes weakly indented ridge on one or both valves (RANSON, 1960, 1967; HU & others, 1993).

Archiheterodonts and euheterodonts are generally characterized by modifications of these hinge types. In some, there may be only small, medial G1a teeth that remain quadrangular or irregular with the provincial ledge tapering posteriorly. G1a teeth may also be absent despite a well-developed P-2 (e.g., in *Hiatella* DAUDIN in BOSC, 1801, and *Cerastoderma* POLI, 1791, 1795), or there may be only two to three unequal teeth of larger size (as in the order Pholadida) (BOYLE & TURNER, 1976; LE PENNEC, 1978; BOOTH, 1979b, 1983).

In general, autobranch bivalves with a cryptoconch or metaconch, or those lacking a P-2, tend to lack G1a hinge teeth or possess only vestiges of these teeth (e.g., philobryids, carditoids, *Lasaea* T. BROWN, 1827; Fig. 23.9–23.12). Unionoid glochidia do not appear to develop provincular taxodont-like teeth; however, some possess interlocking ledges anterior and posterior to the ligament, below the straight hinge line (HOGGARTH, 1999, fig. 5b, 8e, 45c, among others; also barely visible in Fig. 11.1). Larval hinge characters of trigonioids and Protobranchia are unknown, but protobranchs presumably lack G1a teeth, like autobranchs without a P-2 stage.

### Hinge Tooth Generation 1b

Tooth generation 1b (G1b) is the earliest postlarval series of neotaxodont-like teeth in Autobranchia or palaeotaxodont teeth in some Protobranchia. Autobranch G1b either develops as a continuation of G1a (e.g., Fig. 20.2) or appears around the time of metamorphosis, the latter usually in taxa with a metaconch or cryptoconch or without a P-2 (Fig. 24.1–24.2). These teeth or their growth tracks have been described as crenulations, vertical ridges, cancellate area, denticles, crénelles perpendiculaires, or bande crénelée (BERNARD, 1897, p. 9, 12; TEVESZ, 1977; SALAS, 1994; LAMPRELL & HEALY, 1998, p. 72). DELL (1990, p. 26) misinterpreted the philobryid growth tracks of G1b teeth as ligament attachment sites. PREZANT (1990) noted their interlocking function as hinge teeth in the philobryid *Lissarca notorcadensis* MELVILL & STANDEN, 1907 (cf. Fig. 24.3; MALCHUS, 2006).

Mytilids provide the best evidence for a continuity of series G1a into G1b, including some taxa without a P-2 stage (e.g., species of *Crenella* T. BROWN, 1827; *Brachidontes* SWAINSON, 1840; *Septifer* RÉCLUZ, 1848 in 1848–1849; EVSEEV, KOLOTUKHINA, & SEMENIKHINA, 2007; EVSEEV & KOLOTUKHINA, 2008; SEMENIKHINA, KOLOTUKHINA, & EVSEEV, 2008). G1b teeth grow essentially ventralward and may become several tens of

microns high. During this process, smaller G1b teeth often fuse, reaching ~10 µm in length (OCKELMANN, 1983, fig. 26, 28; OCKELMANN, 1995; EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004a, 2004b, 2005). The b-series of OCKELMANN and DINESEN (2009, fig. 2) is apparently equivalent to G1b; the primary teeth of SALAS and GOFAS (1997) include both G1a and G1b. EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005) called this series postprovincular (juvenile) teeth, belonging to the same central morphogenetic (tooth) field as G1a (Fig. 20.1–20.2).

According to EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005), G1b may transform into precardinal and cardinal teeth (10–30 µm, or larger) (Fig. 24.5–24.8; see also pseudocardinal teeth; GALINOUMITSOU & SINIS, 1997, fig. 4). These transformations reflect further successive grades of fusion of G1b teeth, eventually leading to larger, solid teeth. Fusion may also occur between the anterior and posterior tooth ledges so that the resilifer becomes overgrown. Both types of fusion co-occur in some species of *Bathymodiolus* KENK & WILSON, 1985, and *Modiolus* LAMARCK, 1799, after the concomitant onset of ligament 2 and a third, posteriorly developing tooth series (see G1c below; GUSTAFSON & others, 1998, fig. 5; OZAWA & SEKIGUCHI, 2002, fig. 6, 8; OKUTANI, FUJIKURA, & SASAKI, 2003, fig. 5d, 9d).

G1b development in other pteriomorphs has been documented mainly in arcoids, some pteroids, limoids, and pectinoids (e.g., BERNARD, 1896a, 1896b; LE PENNEC, 1978; SALAS, 1994; MALCHUS, 2000a, 2000c, 2000d, 2006; MALCHUS & WARÉN, 2005). Of these, only Jurassic *Atreta* sp. ÉTALLON, 1862, shows a kind of pseudocardinal hinge tooth grade (Fig. 24.4) (cf. MALCHUS, 2000c).

Strongly prosogyrate cyrtodonts *incertae sedis* (Paleozoic ancestors of arcoids) show an asymmetric G1a/b dentition in which a shorter, anterior-central row below the umbo is dorsally overlapped by the proximal teeth of a longer, posterior tooth row (Fig. 25.1; cf. DZIK, 1994, fig. 31, 36). It is noteworthy that published images of these cyrtodonts

do not allow unequivocal distinction of G1a and G1b. However, the morphological disposition mirrors the arrangement of opisthogyrate bakevelliid and ostreoid larval hinges (G1a), as well as that seen in inoceramids and the Silurian modiomorphid (?) *Butovicella* KRÍŽ, 1965, with G1a/b (DZIK, 1994, fig. 32; KNIGHT & MORRIS, 1996, fig. 4; MALCHUS, 2004a).

These examples of inverse (anterior over posterior or vice versa) tooth overlap in different higher taxa and growth stages suggest a universal growth constraint induced by opposed helicoidal growth tendencies: (1) posteriorward coiling giving rise to shells with prosogyrate umbos (e.g., cyrtodontids) and an anterior G1a/b tooth series overlapped dorsally by a posterior series; or (2) anteriorward coiling giving rise to shells with umbos and G1a/b teeth arranged in the opposite direction, as in bakevelliids and oysters (MALCHUS, 2004b, fig. 2). Similar tendencies can also be observed in postlarval opisthogyrate protobranchs (e.g., LA PERNA, 2007a, pl. 5,2c; pl. 6,6; pl. 8,11b, among others) and in postlarval prosogyrate Glyptarcidae (early arcoids) (cf. Fig. 25.2; COPE, 1996, fig. 5; COPE, 1999, pl. 3).

Limopsid and especially philobryid arcoids develop rather extensive growth tracks of G1b teeth by adding numerous teeth along the dorsal shell margin of the early nepioconch and adult shell (PREZANT, 1990; MALCHUS & WARÉN, 2005; MALCHUS, 2006). Along the ventral and distal anterior/posterior areas of these tracks, G1b teeth fade into pustules and vermiculate structures (Fig. 24.3, Fig. 25.3–25.5). BERNARD (1897, p. 29) described these structures as “still well aligned granulations” (our translation). Glycymeridids are comparable to limopsids in this respect (BERNARD, 1896a, fig. 2; MALCHUS & WARÉN, 2005).

Current evidence suggests that philobryid G1 development essentially begins with G1b, although G1a rudiments may be present in some taxa (see Fig. 23.10). The onset of G1 teeth in limopsids is unknown. However, the offset of G1b growth in arcoids

appears to typically occur after the onset of the subsequent G2 series (Fig. 25.7); in some cases, the former series may remain as the only functional hinge dentition (e.g., in *Philobrya* CARPENTER, 1873; see section on Unresolved Developmental Types, p. 43–48, herein). The oldest alleged philobryid, Triassic *Eophilobryoidella sinoanisica* STILLER & CHEN, 2004, has a hypertrophied hinge plate with extensive G1b growth that, except for the enlargement of the plate, is indistinguishable from G1b development in modern *Philobrya* (e.g., *P. brattstromi* SOOT-RYEN, 1957; Fig. 25.3–25.5).

In the pectinids studied by LE PENNEC (1978) and in pteriids (cf. BERNARD, 1896b), G1b teeth derived from G1a appear to be short-lived. Malleid G1b-like ridges are not interlocking and, therefore, are not considered to be teeth (I. TEMKIN, personal communication, 2010). Pectinid and spondylid hinge crenulations are discussed below (see section on Unresolved Developmental Types, p. 43–48, herein).

Unionoids lack G1b teeth. Trigonoids have not been studied in this regard. In the megaorder Cardinata, G1b may persist for a short postlarval period before they become overgrown or incorporated into cardinal G2 teeth (e.g., in the minorder Veneroitei; Fig. 23.7–23.8) (LE PENNEC, 1978; EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004c). Condylocardiid cryptoconchs and metaconchs possess pustular hinge structures reminiscent of G1b precursors, like those in *Philobrya* (Fig. 23.10) and *Lasaea* (Fig. 23.12; see section on Unresolved Developmental Types, p. 43–48, herein). Well-developed G1b teeth in crassatelloids appear to be exceptional [e.g., *Crassatellites* (*Crassinella*) *duplinianus* DALL, 1903a; LABARBERA, 1974, pl. 6.2,7].

Protobranch G1b teeth occur in some *Nucula* LAMARCK, 1799, *Condylonucula* D. R. MOORE, 1977, and *Ennucula* IREDALE, 1931 (BERNARD, 1896a, fig. 10; GOFAS & SALAS, 1996; OCKELMANN & WARÉN, 1998). *Nucula* may also develop a medial row of smaller teeth flanked on both sides by a few larger teeth (possibly G1c) that are still

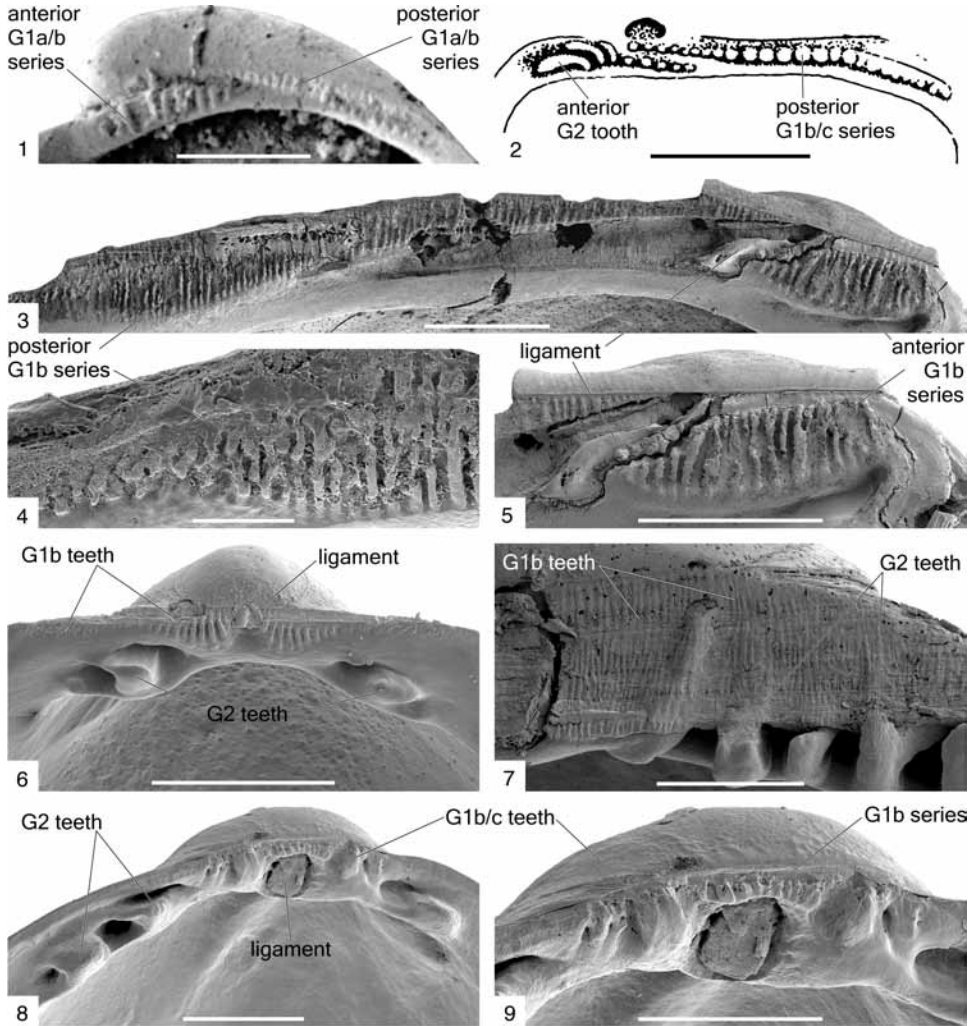


FIG. 25. Examples of G1 and G2 teeth morphologies; 1, right valve of a Silurian cyrtodontid, scale bar, 200  $\mu$ m (adapted from Dzik, 1994); 2, left valve of *Glyptarca serrata* COPE, 1996, drawn from an internal mold, scale bar, 3 mm (adapted from Cope, 1996); 3–5, left valve of *Philobrya brattstromi* SOOT-RYEN, 1957, showing general view of hinge and details of posterior and anterior G1b series, respectively, scale bars: 300, 100, and 300  $\mu$ m, respectively (adapted from Malchus, 2006); 6, *Limopsis aurita* (BROCCHI, 1814), showing G1b teeth fading distally, scale bar, 300  $\mu$ m (adapted from Malchus & Warén, 2005); 7, G1b teeth co-developing with G2 in *Lisarca* sp. E. A. SMITH, 1879, scale bar, 300  $\mu$ m; 8–9, *Nucula* LAMARCK, 1799, species (Antarctic) showing larger teeth (G1b/c) in between the typical G1b and G2 series; also note granular (nonfibrous) resilium, scale bars, 150 and 120  $\mu$ m, respectively (new).

separate from G2 (Fig. 25.8–25.9). Figures in BERNARD (1896a, fig. 12, 14, 15) also suggest the presence of G1b in Miocene *Saccella commutata* (PHILIPPI, 1844) [see *Leda fragilis* (CHEMNITZ, 1784, made unavailable by ICZN, 1944, Opinion 183), in BERNARD, 1896a], and in *Malletia subaequalis* (G. B.

SOWERBY II, 1870a) (see *Malletia hyadesi* ROCHEBRUNE & MABILLE, 1889, in BERNARD, 1896a), but this requires confirmation.

**Hinge Tooth Generation 1c**

Hinge tooth generation 1c (G1c) is the third and last sequence of postlarval

neotaxodont-like teeth, possibly exclusive of mytilids (but see section on Unresolved Developmental Types, p. 43–48, herein). It forms along the posterodorsal shell margin, above the onset position of the second resilifer, and is usually separated by a small gap from the slightly smaller posterior G1b tooth. However, the transition from posterior G1b to G1c appears to be gradual in several *Crenella* species (Fig. 20.2, Fig. 24.5–24.8; OCKELMANN, 1983, p. 115; SALAS & GOFAS, 1997, table 2), and populations of *Dacrydium* cf. *hyalinum* (MONTEROSATO, 1875b) show both distinctly separated and gradational character states (SALAS & GOFAS, 1997). The proximal portion of the G1c series becomes overgrown by ligament 2.

G1c postlarval teeth may be followed by a second posterior sequence before the appearance of posterior dysodont teeth (EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2005; see also below, Mytilid and Pteroid Dysodont G2, p. 39, herein). The two subseries are here distinguished as primary and secondary G1c. The secondary G1c subseries is characterized by an increasingly larger size and a tendency to become less inclined with respect to the shell margin. In *Crenella* T. BROWN, 1827, G1c may grade from neotaxodont-like to slightly chevron-shaped (see ZUSCHIN & OLIVER, 2003, fig. 8.10); Figure 24.8 illustrates an initial chevron-shape. Primary and secondary G1c are often indistinguishable; they belong to the posterior morphogenetic [tooth] field *sensu* EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005).

Small, toothlike structures may also arise on the anterodorsal shell border anterior to and apparently independent from the anterior G1b teeth. These so-called pseudocrenulate or pseudocrenulative teeth and the following dysodont G2 teeth define the anterodorsal field of morphostructures *sensu* EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005). Pseudocrenulative teeth form after the onset of posterodorsal G1c and could reflect a delayed G1c development on the anterodorsal shell margin. The crenulative teeth of EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005) apparently represent shell

margin denticles induced by external ribs; they are not presently considered to be hinge teeth (cf. EVSEEV, KOLOTUKHINA, & SEMENIKHINA, 2007, fig. 3b–c).

Both the G1b and G1c tooth series may expand into the adult stage. According to drawings by GALINOUMITSOU and SINIS (1997, fig. 4), *Lithophaga lithophaga* (LINNAEUS, 1758) displays the entire range of developmental steps from G1a to G1c teeth. This species also shows deterioration structures of both anterior G1b/c and of posterior G1c teeth in later postlarval stages (cf. G1b of philobryids and carditoids). According to OCKELMANN and DINESEN (2009), mytilids lacking a distinct nepioconch stage also lack G1c teeth [e.g., *Adula schmidtii* (SCHRENCK, 1867)]; see EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2005).

Synonyms for the primary G1c are primary lateral teeth (SIDALL, 1980, fig. 1–2; KIMURA & SEKIGUCHI, 1994, fig. 1; EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2005, fig. 1–2), posterior teeth I of the dissoconch (RAMORINO & CAMPOS, 1983, fig. A), minute teeth (SAKAI & SEKIGUCHI, 1992, fig. 2), secondary teeth (SALAS & GOFAS, 1997, fig. 1), and second dorsal series (OCKELMANN, 1983, fig. 53). The secondary G1c teeth are apparently equivalent to cardinal teeth *sensu* SAKAI and SEKIGUCHI (1992) and to the posterior dissoconch teeth II of RAMORINO and CAMPOS (1983). The secondary lateral teeth of SIDALL (1980) could already represent posterior dysodont teeth, as discussed below.

## HINGE TOOTH GENERATION 2

Tooth generation 2 (G2) encompasses most of the traditionally recognized adult hinge dentitions, such as taxodont, dysodont, schizodont, palaeotaxodont, neotaxodont, heterodont, and presumably also pretaxodont (in Cambrian fordilloids). They are distinguished from the G1 series by a rather abrupt change to a larger tooth size and different morphologies. They are generally set off from G1 by a toothless gap, but see cardiomorph composite G2 teeth in section on Unresolved Developmental Types, p. 43–48, herein.

### Mytilid and Pterioid Dysodont G2

The term dysodont was coined by BERNARD (1897, p. 32) for hinge teeth without a proper cardinal area, as in mytilids, philobryids, and ostreids (though the latter may refer to chomata). BERNARD assumed that dysodont teeth are homologous to the “taxodont” teeth of arcoids and protobranchs but “less differentiated” (BERNARD, 1897, our translation).

Mytilid dysodont G2 teeth form on the early adult shell margin close to but independent of G1b or G1c, if the latter is developed (Fig. 20.3–20.4). On the anterodorsal margin, they develop as short and somewhat wavy bosses on a shell shelf; they eventually overgrow the postprovinculum and become either better defined or reduced. Posteroventral G2 teeth are often formed as elongated, wavy ledges with a tendency to become subparallel to the shell margin. They usually disappear before the anterodorsal G2 tooth row does.

Absence of dysodont teeth appears to be a consequence of small adult size or heterochrony and is commonly observed in species that lack a P-2 stage (e.g., *Dacrydiini*, *Crenellini*; see Fig. 24.6–24.8). Similar dysodont-like structures of philobryids are discussed below in the section on Unresolved Developmental Types (p. 43–48, herein).

Recent pterioids typically develop a few, inconspicuous G2 teeth below the ligament area (Fig. 22.1), rather than on the shell margins anterior and posterior of G1 teeth as in mytilids [see small adult *Bakevellia gibbera* (FARSAN, 1972), in MUSTER, 1995, pl. 4, 14, among others]. Pterioid G2 ontogeny is essentially independent of G1 development and may be restricted to the juvenile shell stage (e.g., *Isognomon* LIGHTFOOT, 1786; see BERNARD, 1896b, fig. 9, 10, 5LV, 10, 5RV, and 10, 6RV; BERNARD, 1898, pl. 9; COX & others, 1969, fig. C50, 2c–e). The extinct *Bakevelliidae* provide examples of numerous and rather distinct G2 teeth, in addition to smaller teeth, some of which may belong to the earlier G1 tooth series (COX & others,

1969, fig. C40; MUSTER, 1995, pl. 1, 6–7; pl. 5, 14; pl. 16, 10–12; pl. 17, 1–5). In apparently rare cases, bakevelliids may also show vertical ridges on the posterior laterals (MUSTER, 1995, pl. 17, 3), reminiscent of arcoid G2 tooth development (see below). It appears likely that tooth development of many older Paleozoic pteriomorphs (as well as cycloconchids) could be homologous with that of bakevelliids and pterioids; however, the early developmental patterns are still largely unknown.

### Arcoid G2

As in other pteriomorphs, the neotaxodont G2 tooth development of arcoids begins in the early postlarval stage. However, it may follow two different ontogenetic pathways. In limopside, glycymeridid, philobryid, and cucullaeid (e.g., *Cucullaea* LAMARCK, 1801), G2 teeth do not show any constructional overlap with G1 teeth, but the older tooth series (G1b) still develops further at least for some time during juvenile growth and expands ventralward together with the advancing edge of the hinge. This creates vertical, sometimes converging, relict growth traces on the ligament area. While this is happening, older portions of G2 teeth may become over-roofed by the hinge and ligament area, if interumbonal growth is strong (BERNARD, 1896a, 1896b; TEVESZ, 1977; MALCHUS & WARÉN, 2005). Occasionally, this growth pattern causes the hinge to bulge above the G2 path (Fig. 25.7).

The second type of tooth development in arcoids is displayed by parallelodontids. Here, the tooth lamellae are formed by progressively filling interspaces between rows of pustular teeth with new shell material. Repetition of this process perpendicular to a lamella leads to the gradual formation of striae on one or both flanks of a lamellar tooth (Fig. 22.2–22.3). Such striate teeth may be filled further during ontogeny until the lamellae are completely smooth. The Ordovician Glyptarcidae seem to have the same type of development (cf. COPE, 1999, pl. 3), but whether this characterizes all

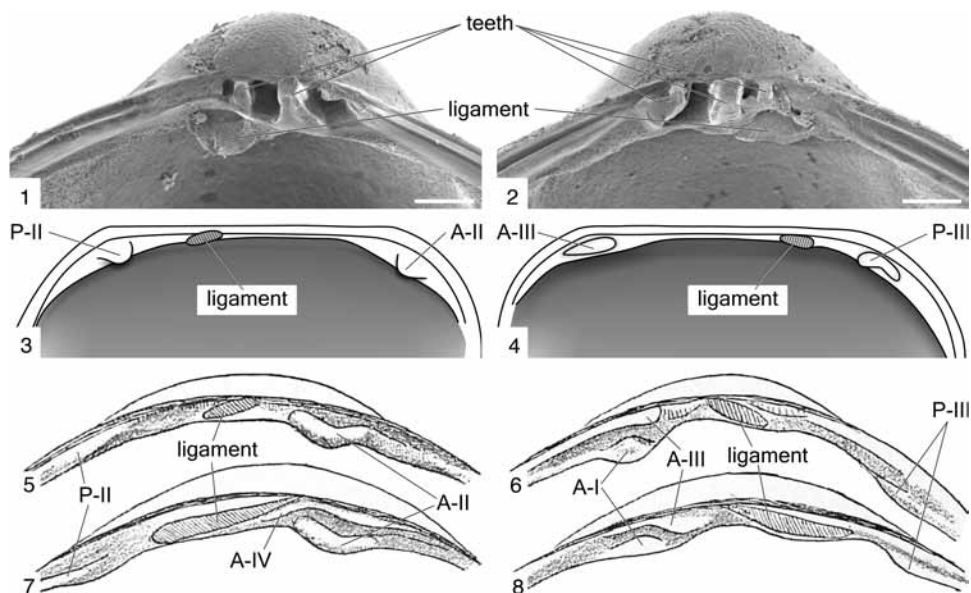


FIG. 26. Early ontogeny of hinge; 1–2, hinges of left and right valves of an early postlarval xylophagine dwarf male, scale bars, 20  $\mu\text{m}$  (new); 3–4, *Gaimardia trapesina* (LAMARCK, 1819 in 1818–1822), hinges of the left (view 3) and right (view 4) early ontogenetic shell valves of a brooded specimen measuring 550  $\mu\text{m}$ ; 5–8, *Kidderia pusilla* (GOULD, 1850b), hinges of left and right early ontogenetic shell valves of specimens measuring 0.8 mm (views 5–6) and 1.2 mm (views 7–8) (views 3–8 adapted from Bernard, 1895).

arcoid lamellar teeth is presently unknown (see discussion of cardiomorph composite G2 teeth in section on Unresolved Developmental Types, p. 43–48, herein).

### Pectinid G2

Pectinids possess various symmetrical lamellar G2 on each side of the ligament (BERNARD, 1896b, fig. 11; WALLER, 1991, fig. 6). Their position ventral of the ligament area is somewhat reminiscent of pterioidean G2 teeth. Although these lamellae appear smooth, they are actually subdivided by microscopic vertical ridges and grooves. This constructional pattern seems to represent yet another type of composite tooth development, but the origin of these microcrenulations is still unclear (see section on Unresolved Developmental Types, p. 43–48, herein).

### Palaeoheterodont G2

The early ontogenies of trigonioid schizodont and unionoid pseudoheterodont

and pseudotaxodont G2 teeth are presently unknown. However, schizodont and pseudotaxodont teeth may be comparable to the composite G2 type of parallelodonts or carditoids. Given the present lack of knowledge, early palaeoheterodont tooth development is only briefly addressed and in a theoretical framework (see section on Unresolved Developmental Types, p. 43–48, herein).

### Heterodont G2

Heterodont G2 teeth ontogeny has been studied in some Carditida and in a larger number of Euheterodonta, mainly members of the minorder Veneroitei (e.g., BERNARD, 1895, 1896d; REES, 1950; LE PENNEC, 1973, 1978, 1980; LUTZ, GOODSSELL, & others, 1982; LUTZ, MANN, & others, 1982; LUTZ, 1985; GOODSSELL & others, 1992; SAKAI & SEKIGUCHI, 1992; EVSEEV, KOLOTUKHINA, & SEMENIKHINA, 2001; EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004c); for additional data, see JØRGENSEN (1946)



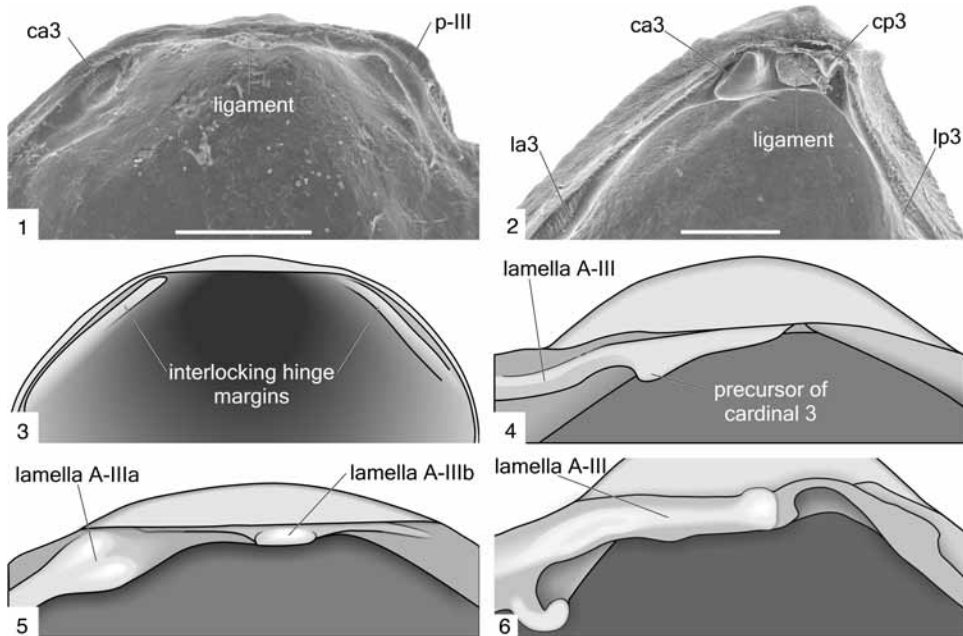


FIG. 27. Early ontogeny of heterodont G2 teeth; 1, right valve of early ontogenetic shell of *Condylocardia digueti* LAMY, 1917, scale bar, 100  $\mu$ m (new); 2, right valve of adult shell of *Condylocardia digueti*, scale bar, 200  $\mu$ m (new); 3, *Chione cancellata* (LINNAEUS, 1767 in 1766–1767), right valve of a prodissoconch-2, showing interlocking hinge margins that are precursors of lamellar teeth, shell length, 186  $\mu$ m; 4, *Chione cancellata*, hinge of right valve of early postlarva, shell length, 404  $\mu$ m; 5–6, *Pitar morrhuanus* (DALL, 1902), hinge of right valve of early postlarval shells (213 and 288  $\mu$ m in shell length, respectively), showing fusion of two teeth to form lamella A-III (views 3–6 adapted from Goodsell & others, 1992).

and ZAKHVATKINA (1959). The more recent literature shows that G2 tooth development generally begins before metamorphosis in species with a P-2, rather than in the postlarva. These studies also point to constructional overlap between heterodont G1 and G2 tooth series, which is reminiscent of features found in pteriomorphs but not well understood. Present observations indicate that G2 development is delayed in taxa with a metaconch or cryptoconch and in those lacking a P-2. As discussed below, metaconchs and cryptoconchs are typical shell types of long-term brooders. Assuming that hinge teeth serve to ensure proper alignment upon adduction of the valves and thus protection of free-living larvae against predation and external hazards, we speculate that brooded taxa are already protected against these factors, so they do not need functional teeth before release. This section gives a brief

summary of general tendencies as well as some special cases, which provides necessary background information for subsequent sections on unresolved developmental types and the homology of tooth series.

In the minorder Veneroitei, the postlarval tooth lamella A-III (RV) derives from the interlocking hinge margin of the prodissoconch-2, and a dorsal swelling of it or a small protuberance directly connected to it develops into cardinal tooth 3 (Fig. 27.3–27.4; see also Fig. 23.6, Fig. 26.8). This initial state may also consist of two disconnected teeth, one anterodorsal and the other below the provinculum, which later fuse, as in *Pitar morrhuanus* DALL, 1902 (Fig. 27.5–27.6); see also BERNARD, 1895, “*Cytherea deshayesiana*” auct., fig. 12, =COX & others, 1969, fig. 48.1, *Gouldia deshayesiana* (BASTEROT, 1825). Similarly, the corresponding tooth lamella A-II of

the left valve usually has a larval origin and may develop before or after A-III. In contrast, precursors of cardinals 1 and 4 typically appear after metamorphosis (LE PENNEC, 1973, 1978, 1980); note that LE PENNEC (1978, 1980) numbered hinge teeth according to their ontogenetic appearance—that is, tooth 1 corresponds to cardinal A3 of BERNARD (1895) and tooth 3 is cardinal A1 of BERNARD; left valve teeth 2 and 4 are the same in both schemes.

Posterior tooth lamellae develop in a comparable fashion (BERNARD, 1895, fig. 21, 23; SAKAI & SEKIGUCHI, 1992; EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004c). EVSEEV, SEMENIKHINA, and KOLOTUKHINA (2004c) also showed how early postlarval G1b teeth become integrated into lamellae A-III and P-III (Fig. 23.7–23.8).

Members of the superfamilies Veneroidea, and especially Arcticoidea, show more complex G2 developmental patterns (LUTZ, GOODSSELL, & others, 1982; LUTZ, MANN, & others, 1982; GOODSSELL, & others, 1992; SAKAI & SEKIGUCHI, 1992, summarized in EVSEEV, SEMENIKHINA, & KOLOTUKHINA, 2004c) [cf. BERNARD, 1895, “*Cyprina islandica*” (LINNAEUS, 1767 in 1766–1767), fig. 14]. In *Cerastoderma* POLI, 1791, 1795 (Cardioidea), interlocking hinge margins develop at a very early P-2 stage but almost disappear in older P-2; precursors of cardinal teeth 3, 2, 1, and 4 form, in that order, relatively late after metamorphosis. Larval *Hiatella* DAUDIN in BOSCH, 1801 (Hiatellida, Solenata) develops only the precursor of lamella A-III. Shortly after the P-1 stage, *Pholas* LINNAEUS, 1758 (Pholadida, Pholadata) generates two tooth protuberances on each valve, one anterior and one posterior to the provinculum, which are disconnected from the interlocking hinge margins. The right posterior tooth becomes a thickened ledge in the postprovinculum (LE PENNEC 1978, 1980). Tooth development in Xylophagidae PURCHON, 1941 (*non* FALLÉN, 1810; see BOUCHET & ROCROI, 2010, p. 89) and Teredinidae, sister-groups according to DISTEL and others (2011), is similarly disconnected from the margins (but with three teeth

in the RV). These teeth probably become overgrown in later growth stages of all three groups. However, they remain functional in dwarf males of Xylophaginae (Fig. 26.1–26.2) and possibly other pholadoids. Their assignment to either G1 or G2 is contentious (cf. LUTZ & JABLONSKI, 1978a, on a juvenile pholadid species from the Cretaceous).

The earliest developing teeth in veneroid metaconchs and cryptoconchs are apparently postlarval, with lamellae A-III, P-III (RV) and A-II, P-II (LV); however, these teeth may or may not be connected to the dorsal shell margins anterior and posterior of the postprovinculum. Overlap with the G1 teeth series is presently unknown in these taxa (Fig. 26.3–26.8).

In the order Carditida (Archiheterodonta), hinge tooth development begins within the prerelease postlarvae, as in Condylocardidae. The first G2 teeth to appear are arched lamellar teeth on the dorsal margins of the metaconch or cryptoconch (RV: A-V, P-III, and LV: A-IV, P-II; Fig. 27.1; BERNARD, 1896c, fig. 2–4; present interpretation). Cardinals CA3 (RV) and CP2 (LV) form as protuberances or short ledges, ventral to and independent from the dorsal lamellae, whereas CA4 and CP3 develop from lamellar A-IV and P-III, respectively. This general pattern is complicated by a lack of understanding of the constructional interrelationship with a marginal G1b/c-like tooth series (see discussion in section on Unresolved Developmental Types, p. 43–48, herein).

### Protobranch G2

In juveniles of *Nucula* LAMARCK, 1799, the first teeth of the G2 series may measure ~20–35  $\mu\text{m}$  in width. In *Austronucula perminima* (MONTEROSATO, 1875a) (= *N. recondita* GOFAS & SALAS, 1996), which first develops G1b teeth (measuring 10 to 16  $\mu\text{m}$ ), the G2 series arises as abruptly larger teeth (starting at ~25  $\mu\text{m}$ ), which are spatially set off from G1b (GOFAS & SALAS, 1996; OCKELMANN & WARÉN, 1998, fig. 4a–c). Subsequent G2 teeth may already measure 40 to 65  $\mu\text{m}$  in both species. In

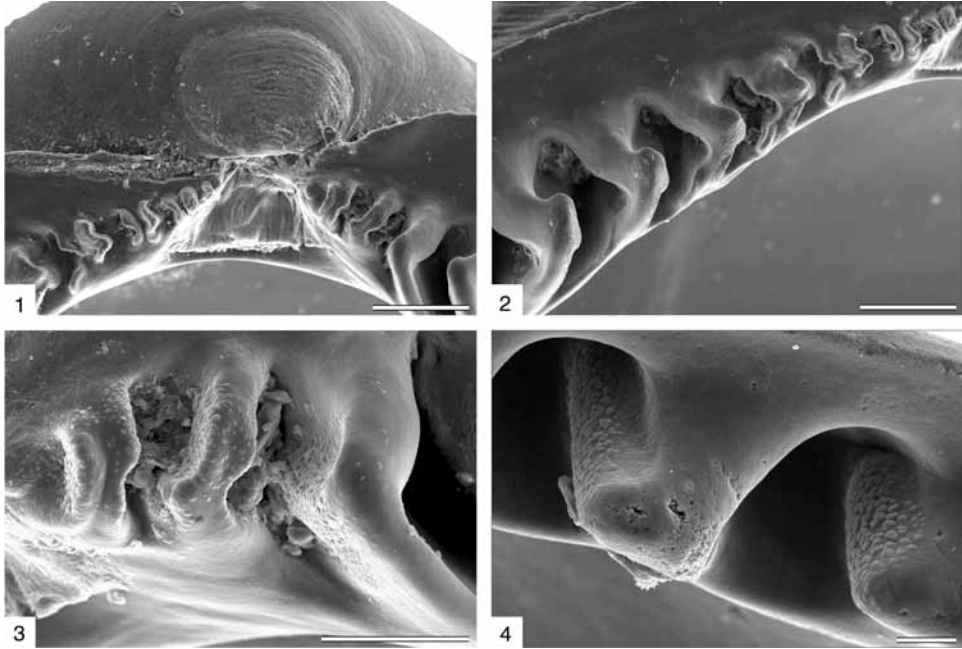


FIG. 28. Postlarval tooth development in Nuculanidae. 1–3, *Nuculana pella* (LINNAEUS, 1758), right valve of small adult; 1, ligament and hinge teeth in the vicinity of the beaks, scale bar, 100  $\mu\text{m}$ ; 2, anterior hinge teeth series, showing gradual fusion of teeth toward the anterior end, scale bar, 100  $\mu\text{m}$ ; 3, detail of three teeth of the posterior series, showing pustular surface sculpture, scale bar, 50  $\mu\text{m}$ ; 4, Jurassic *Mesosaccella* CHAVAN, 1946, species, showing G2 teeth with a pustular dorsal surface, scale bar, 10  $\mu\text{m}$  (new).

*Nucula* sp., from Antarctic waters, initial G2 tooth size is about 50  $\mu\text{m}$ . As far as known, nuculid G1b teeth are not fused and lack pustulation (cf. Fig. 25.8–25.9).

The extant Solemyidae lack hinge teeth at all shell stages (GUSTAFSON & REID, 1986), although some Paleozoic species may retain vestiges of subumbonal palaeotaxodont teeth in the left or right valve (CARTER, 1990, p. 177; BAILEY, 2011). Members of the closely related family Manzanellidae (=Nucinelidae) possess what appear to be G2 teeth (ALLEN & SANDERS, 1969; ALLEN & HANNAH, 1986; LA PERNA, 2004; OLIVER & TAYLOR, 2012).

Postlarval tooth development in Nuculanidae seems to start with small G2 teeth measuring  $\sim 10 \mu\text{m}$  in width. Unlike nuculids, subsequent teeth grow by fusion of two principal and one or two adventitious teeth. This process generates short chevron-

shaped teeth (Fig. 28); however, these subdivisions disappear from the 8th tooth onward (approximately). In addition, the earlier formed teeth have a pustular substructure that remains preserved as pustular surfaces on the dorsal flanks of the larger, fused teeth. These pustules do not show the typical vertical alignment as in parallelodontid Arcida and in Archiheterodonta (e.g., Carditida).

#### UNRESOLVED DEVELOPMENTAL TYPES

This section discusses hinge dentitions whose origins remain unclear. The variety of these structures suggests that early postlarval hinge tooth development in Bivalvia is more complex than currently appreciated.

#### Philobryid Dysodont or Arcoid G2 Teeth

The difficulties in homologizing philobryid hinge teeth with those of other bivalves

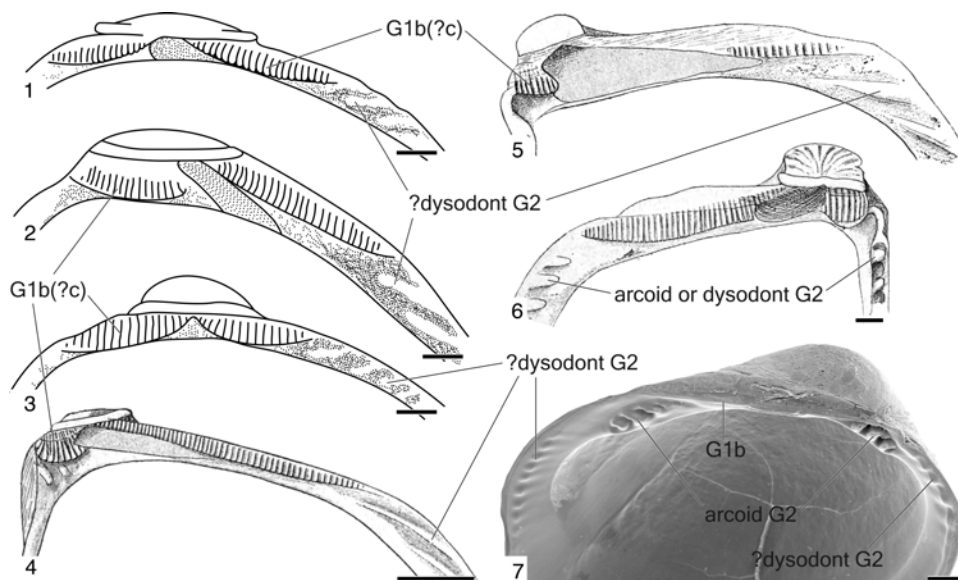


FIG. 29. Hinge structure of selected philobryids; 1, *Hochstetteria trapezina* BERNARD, 1897, right valve, scale bar, 100  $\mu$ m; 2, *H. modiolina* VÉLAIN, 1877, right valve, scale bar, 100  $\mu$ m; 3, *H. crenella* VÉLAIN, 1877, right valve, scale bar, 100  $\mu$ m; 4, *Philobrya munieri* BERNARD, 1896c, right valve, scale bar, 500  $\mu$ m; 5, *Cosa filholi* (BERNARD, 1897), right valve, no indication of scale; 6, *C. costata* (BERNARD, 1896c), left valve, scale bar, 100  $\mu$ m (views 1–6, adapted from Bernard, 1897); 7, *Lissarca miliaris* (PHILIPPI, 1845), left valve, scale bar, 300  $\mu$ m (Malchus & Linse, new).

are well reflected by BERNARD (1896b, p. 423) who, largely based on hinge dentition and shell outline, placed the philobryid genus *Hochstetteria* VÉLAIN, 1877 (*sensu* BERNARD) closer to Mytilidae and later Pteriidae than to Arcidae (cf. BERNARD, 1897, p. 8, Aviculidae: Philobryinae) (note that Aviculidae = Pteriidae, order Ostreida, and Philobryinae is raised to family rank within order Arcida; cf. CARTER & others, 2011). In the three species of *Hochstetteria* studied by BERNARD (1897, fig. 3, 6), the most distal posterior dentition is set off from the earlier G1b (or G1c?) series and may represent either dysodont G2 or small arcoid G2 teeth (Fig. 29; see Fig. 20.3–20.4). HUBER (2010) placed *H. trapezina* BERNARD, 1897, and *H. crenella* VÉLAIN, 1877, in the genus *Adacnarca* PELSENEER, 1903, but he placed *H. modiolina* VÉLAIN, 1877, in the genus *Philobrya* CARPENTER, 1873.

Similarly, in *Philobrya munieri* (BERNARD, 1896c), *P. atlantica* DALL, 1896, and *Cosa filholi* (BERNARD, 1897), the second tooth

series is reminiscent of mytilid dysodont-like teeth, whereas that of the type species of *Cosa*, *C. costata* (BERNARD, 1896c), seems to compare better to arcoid G2 teeth [note that TEVESZ (1977, p. 12) did not distinguish this tooth series in *Cosa*]. Furthermore, *Lissarca* E. A. SMITH, 1879, apparently develops three sets of teeth, of which the weaker one is dysodont-like in its marginal rather than inframarginal position. This set may, however, represent the initial growth of internal radial ribs; observations of various growth stages show that it develops after the G2 series (e.g., in *L. notorcadensis* MELVILL & STANDEN, 1907; Fig. 24.3).

#### Arcid and Cucullaeid G1-Like Teeth and Dental Fusion

The broad hinge plates of arcids and cucullaeids show continuous vertical striations, which are not ligament-related ridges and troughs (see pseudotrabeulae as in *Noetia* Gray, 1857 in 1853–1857; CARTER & others, 2012, fig. 181), but closely resemble

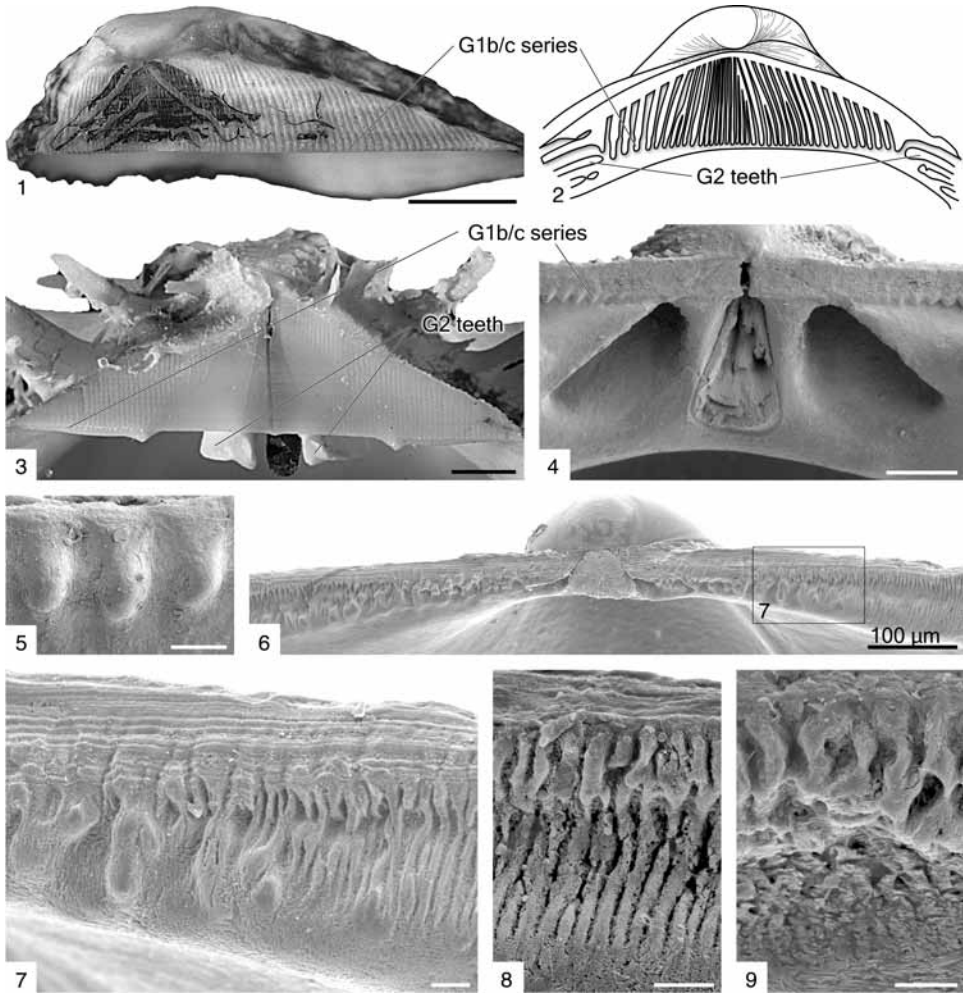


FIG. 30. Examples of arcid, cucullaeid, and pectinoid hinge dentition and crenulations; 1, *Arca noae* LINNAEUS, 1758, dorsal view of right valve after partial removal of ligament cover, scale bar, 1 cm (new); 2, *Cucullaea crassatina* LAMARCK, 1801, hinge showing supposed vertical G1b teeth, ventrally in contact (possibly fused) with G2 teeth (left), no indication of scale (adapted from BERNARD, 1896a); 3, *Spondylus wrightianus* CROSSE, 1872, FMNH 318143, hinge of right valve, showing G1b/c teeth and their growth traces above G2 teeth, scale bar, 2 mm; 4–5, *Spondylus wrightianus* CROSSE, 1872, NHMUK 20010929, hinge of left valve, showing the G1b/c tooth series; 4, general view, scale bar, 500  $\mu$ m; 5, detail, scale bar, 100  $\mu$ m; 6–7, *Mimachlamys varia* (LINNAEUS, 1758), hinge of left valve; 6, general view, scale bar, 100  $\mu$ m; 7, detail of area delimited by a rectangle in view 6, scale bar, 10  $\mu$ m; 8, *Palliolium incomparabile* (RISSO, 1826), crenulations along hinge plate, scale bar, 10  $\mu$ m; 9, *Aequipecten opercularis* (LINNAEUS, 1758), crenulations along hinge plate, scale bar, 10  $\mu$ m (new).

the neotaxodont-like G1b dentition of limopsids and philobryids. However, unlike these latter taxa, arcid G1b/c are 50  $\mu$ m wide in early juveniles of *Anadara diluvii* (LAMARCK, 1805 in 1802–1806) (cf. G1c teeth of mytilids) and 250–500  $\mu$ m wide in adult *Arca noae* LINNAEUS, 1758 (cf. Fig.

30.1; BERNARD, 1896a, fig. 5; 1896b, fig. 13). Their growth tracks, visible on the hinge plate after removal of the ligament cover, can be traced back to the adult umbo. Similar teeth in the Tertiary *Cucullaea crassatina* LAMARCK, 1801, are followed by a well distinguished G2 series, which, however,

seems to conflict spatially and partially fuse with G1b (or G1c?). The origin of these G1b-like teeth and their role in G2 development, if any, remains obscure.

### Spondylid G1b-Like Teeth

Similarly to *Arca* LINNAEUS, 1758, spondylids develop G1b-like growth traces over the entire height of the hinge area, which end in a finely toothed leading edge of the hinge margin. Tooth width appears to range from ~50 to 250  $\mu\text{m}$  (cf. Fig. 30.3–30.5; BERNARD, 1896b, fig. 13; 1896a, fig. 5). Their origination phase has not been studied. However, unlike *Arca*, spondylids develop an independent, isodont G2 tooth series that becomes dorsally overarched by the advancing hinge area. This arrangement is comparable to *Lissarca* sp. (Philobryidae) and, therefore, suggestive of larger G1b or perhaps G1c teeth (Fig. 30.3–30.5).

### Pectinid and Spondylid Hinge Crenulations

CHECA, ESTEBAN-DELGADO, and SALAS (2011, p. 344) defined hinge crenulations as a “. . . succession of micron-sized elongated ridges and troughs with a general dorsoventral pseudolabyrinthine pattern that are present on the hinge plate of most Pectinoidea. The crenulations of opposing valves are complementary and interpenetrate in a hinge-like fashion.” Pectinid crenulations dissect the lamellar G2 teeth and troughs; spondylids lack tooth lamellae, and the crenulations are found on the hinge plate and its ventral margin (see section on Arcid and Cucullaeid G1-like teeth and dental fusion, p. 44, herein). The so-called pseudolabyrinthine pattern refers to elongated, vermiculate, and more or less irregularly bounded pustular structures.

Histological analysis of pectinid hinge crenulations by CHECA, ESTEBAN-DELGADO, and SALAS (2011) shows that mantle cells only adhere to the ridges, and that cells secreting the ridges have a more complex internal structure indicative of higher metabolic activity than those facing (but not adhering to) the

troughs. The authors suggested that these crenulations are unrelated to the provinculum, a claim that has not been supported by examination of larval to early postlarval shells. Observations of early postlarvae suggest that the ridges could represent substructures of G1b- or G1c-like hinge teeth (Fig. 30.6–30.9). CHECA, ESTEBAN-DELGADO, and SALAS (2011) compared these structures with those of fossil Euchondriidae (COX & others, 1969, fig. C65, *1b*) and Recent Spondylidae, both of which possess either well-defined G1b-teeth (similar to those of *Philobrya*) or pustular to vermiculate G1b/c-like structures.

### Ostreoidan Chomata

Chomata are ridge and trough features that typically occur on the dorsal commissure of many oyster shells. They may be straight or vermiculate (labyrinthic), and both types may degenerate into pustules, forming patterns reminiscent of the hinge crenulations described above. However, unlike most of those features, chomata sizes range from about 150 to 2000  $\mu\text{m}$  in adult shells, and they may occur circumferentially around the entire commissure (Fig. 31). HARRY (1983, 1985) observed their correspondence to epithelial mantle structures, which he called proto-chomatal bands. In addition to pustular chomata, the lophine genus *Alectryonella* SACCO, 1897, possesses fine, fingerprint-like shell threads on the depositional surface (also present in some Pycnodonteinae and Exogyrinae), which BISHOP (1984) interpreted as drainage patterns. However, their morphology seems compatible with shell imprints of proto-chomatal bands, and some of these threads end with a chomatal ridge or pustule. Whether these features share any developmental relationship or represent relics of a true tooth series is presently unknown.

### Carditoid G1b/c and Composite G2 Teeth

The early postprovinculum of carditoids has irregular pustules that develop into better defined G1b-like teeth [cf.

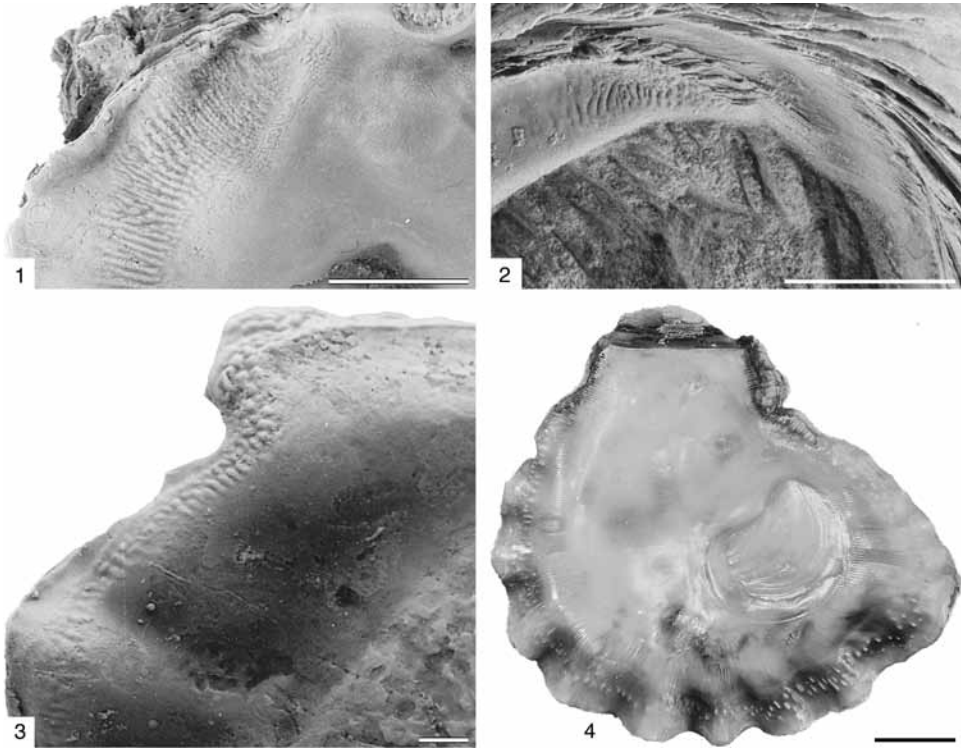


FIG. 31. Chomata in selected osteoids; 1, *Costeina costei* (COQUAND, 1869) (Pycnodonteinae), with elongated chomatal ridges, some of which disintegrate and become slightly vermiculate; most dorsal chomata are affected by silicification diagenesis (beekite rings) and, thus, are not representative, scale bar, 10 mm; 2, *Exogyra overwegi* VON BUCH in BEYRICH, 1852 (Campanian), showing short, slightly vermicular chomata, scale bar, 10 mm; 3, *Gryphaeligmus jabbokensis* (COX, 1925) (Jurassic), with straight (lower left) chomata disintegrating into rows of pustules toward top (dorsal), scale bar, 1 mm; 4, *Alectryonella* SACCO, 1897, species showing pustule chomata, fingerprint shell structure, and protochomatal bands, scale bar, 10 mm (new).

LABARBERA, 1974, pl. 6,2,7, *Crassatellites* (*Crassinella*) *duplinianus* DALL, 1903a]. On the lateral lamellae (G2 series), these teeth become short and vermiculate to pustular. Subsequently, the tops and flanks of the cardinal teeth, tooth lamellae, and lateral teeth reveal stacked pustular subunits that form vertical striations. These subunits may disintegrate further into isolated shell protuberances. Therefore, it appears that carditoid hinge tooth development consists of vestigial to advanced G1b (or also G1c) stages that then become integrated into G2 teeth (Fig. 32; cf. SALAS & ROLÁN, 1990, fig. 24; MIDDELFART, 2002a, 2002b). The observed growth patterns are reminiscent of three developmental modes: (1) G1b-fusion

into a club-shaped pseudocardinal tooth as seen in some mytilids (e.g., SALAS & GOFAS, 1997, p. 279, fig. 63, *Dacrydium* TORELL, 1859); (2) the stacked pustule pattern of parallelodontid G2 teeth; and (3) the disintegration of G1b teeth into vermicules and pustules as, for example, in philobryid Arcida (Fig. 25). However, these substructures usually become indistinct in fully grown specimens (Fig. 32).

#### Palaeoheterodont G2 Subdivisions

The schizodont G2 teeth of adult Trigoniidae are vertically ridged. STANLEY (1977) referred to the G2 teeth as primary and to their ridges as secondary teeth. Although this scheme reflects their functional

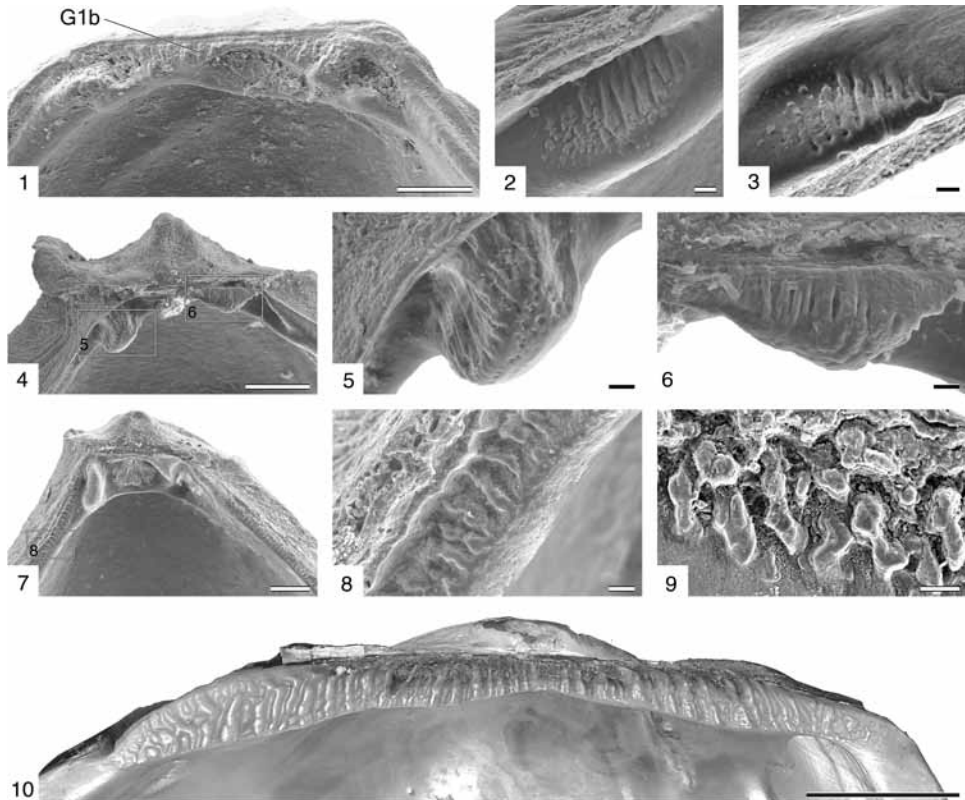


FIG. 32. G1b and composite G2 teeth in selected carditid, condylocardiid, and unionid hinges; 1, carditid hinge of *Carditella naviformis* (REEVE, 1843), showing well-developed G1b teeth, scale bar, 50  $\mu\text{m}$  (Malchus & Linse, new); 2, *Condylocardia geigeri* COAN, 2003, showing either various levels of disintegration of ridges into pustules or of fusion of pustules into ridges (both views may be correct), scale bar, 10  $\mu\text{m}$ ; 3–6, *C. hippopus* (MÖRCH, 1861 in 1859–1861); 3, top view reveals that lateral ridges are not yet entirely fused to make a lamella, scale bar, 10  $\mu\text{m}$ ; 4, scale bar, 100  $\mu\text{m}$ ; 5, detail of area delimited by corresponding rectangle in view 4, scale bar, 10  $\mu\text{m}$ ; 6, detail of area delimited by corresponding rectangle in view 4, scale bar, 10  $\mu\text{m}$ ; 7–8, *C. digueti* LAMY, 1917; 7, scale bar, 100  $\mu\text{m}$ ; 8, detail of area delimited by rectangle in view 7, scale bar, 10  $\mu\text{m}$ ; 9, *Philobrya meleagrina* (BERNARD, 1896c), detail of disintegrating G1b teeth for comparison, scale bar, 10  $\mu\text{m}$  (new); 10, hinge teeth of adult shell (LV) of *Pleiodon ovatus* (SWAINSON, 1823), scale bar, 15 mm (views 2–9, new; view 10, van Damme, new).

significance, there is presently no evidence that schizodont teeth precede the vertical striations ontogenetically. To the contrary, the similarity of these ridges to those of adult parallelodontid lamellar teeth, as well as to carditoid composite G2 teeth, could indicate similar early developmental pathways. Both hypotheses remain speculative until further study.

Unionoid adult hinges provide similar doubtful cases. The lack of G1 teeth in their glochidia and postlarval shells would seem to discourage any hypothesis of correlation

between the heterodont-like G2 of the adults and a G1 generation. Yet, iridinid Mullerioidea develop a kind of neotaxodont G2 dentition and vermiculate structures reminiscent of G1b (or G1c?) teeth of philobryids and carditoids (Fig. 32.10) (cf. COX & others, 1969, fig. D55,4–D55,5; MORRIS & FORTEY, 1976, p. 707, fig. 4A; GRAF & CUMMINGS, 2006, fig. 6E, *Pleiodon* CONRAD, 1834). The prevailing opinion that unionoid adult hinge teeth represent convergent developments may therefore require reassessment.



## HOMOLOGY OF TOOTH SERIES

### Autobranch Provincular Teeth (G1a)

The development of provincular (G1a) teeth is strictly tied to the presence of a prodissoconch-2 stage, which is in turn linked to the presence of a larval velum and planktotrophy. Given that current evidence favors the lack of a two-staged larval shell in Cambrian mollusks (NÜTZEL, LEHNERT, & FRYDA, 2006, 2007; RUNNEGAR, 2007), it appears that the prodissoconch-2, coupled with the velum and a free-swimming planktotrophic life cycle, are apomorphic features of autobranch bivalves. This view, which implies an independent origin from the protoconch 2 of gastropods, is consistent with the known fossil record of larval shell types and hinges.

### Autobranch Postprovincular Teeth (G1b-c)

Ample evidence from pteriomorphian, archiheterodont, and euheterodont bivalves suggests that the G1b series is the early post-larval continuation of the G1a series; in addition, G1c shows essentially the same growth pattern and continuity with G1b, at least in some mytilids. G1a through G1c are, therefore, viewed as a successive subseries controlled by a common morphogenetic growth field. In autobranchs lacking a P-2 (or with a metaconch or cryptoconch), activation of this growth pattern begins after metamorphosis and shortly before birth—that is, before release from the mother. This may be attributed to long-brooding or heterochronic processes, or both. Such so-called losses occur independently in numerous living taxa.

The G1b/c-like teeth of spondylids and arcids, hinge crenulations of pectinids and spondylids, as well as chomata in Ostreioidea and other pteriomorphian lineages cannot presently be confidently homologized with a G1b or G1c series. Nonetheless, spondylids produce a separate G2 series, suggesting that previous teeth derive from G1b or G1c. Similarly, neotaxodont tooth development in Arcidae may be comparable to Philobry-

oidea, in which adult teeth can either belong to G1b, as in *Philobrya* CARPENTER, 1873, or to the G2 series, as in *Cratis* HEDLEY, 1915; *Limopsilla* THIELE, 1923; or *Lissarca* E. A. SMITH, 1879, among others. The presence of G2 teeth appears to be plesiomorphic in this group (cf. G2 of Limopsidae and Glycymerididae), whereas suppression of their development could be autapomorphic for each taxon.

### Autobranch G2 Tooth Series

Early patterns of G2 development in Autobranchia do not provide clear evidence of successive ontogeny; for this reason, they cannot presently be divided into subseries of a single homologous feature. To the contrary, G2 development produces four or five apparently unrelated types of composite teeth in Pectinida, Arcida, Carditida, Unionida, and possibly Trigoniida, as well as several apparently compact types, including the dysodont teeth of Mytilidae and Pterioidea, G2 teeth of most Arcida, and heterodont teeth of the megaorder Cardiata (=Neoheterodontei of TAYLOR & others, 2007).

Except for parallelodontids and Arcida, composite teeth seem to emerge from a constructional overlap with the G1b/c series, a pattern that could have occurred convergently depending on the evolution of reproductive modes and correlated heterochronic processes in each clade. The lack of such overlap may thus give rise to the compact G2 type. These speculations demonstrate the need for more detailed observations.

Since REES (1950), it has also become increasingly clear that G2 development in the Cardiata begins in the prodissoconch-2, and that developmental variety is more complex than assumed previously. However, a thorough review of G2 homologies in Cardiata requires an in-depth analysis of the entire developmental path, which lies beyond the scope of this chapter.

### Protobranch Hinge Teeth (G1b, 2)

The origin, early ontogeny, and evolution of the protobranch hinge dentition remain

obscure, although it appears clear that functional larval G1a teeth are absent, as in those Autobranchia lacking a P-2 or displaying metaconchs or cryptoconchs. The G1b teeth of nuculids have been interpreted as haphazard paedomorphic structures (GOFAS & SALAS, 1996, p. 434), which implies that they represent the ancestral character state within a nuculid lineage or the entire family. Yet, if BERNARD correctly indicated the presence of small postprovincular (G1b) teeth in Nuculanidae (cf. BERNARD, 1896a, fig. 12, 15), the character could be a symplesiomorphy of the two protobranch taxa or of Protobranchia and Autobranchia. Until further studies can test these hypotheses, homology assumptions for protobranch G1 and thus also G2 teeth must remain speculative (see next section).

#### The G1-G2 Developmental Pattern

A bi-modular (G1-G2) pattern of hinge teeth development is here considered plesiomorphic within autobranchs. In planktonic-planktotrophic species, it is typically preserved as G1a-G2. Long-brooding taxa lack G1a but typically develop the G1b/c-G2 pattern. As explained above, the lack of G1a teeth in nonplanktonic taxa is related to the absence of a prodissoconch-2. Similarly, G2 teeth reduction often occurs in conjunction with long-brooding and miniaturization; in some groups this reduction appears to be compensated by a so-called hypertrophied G1b series that remains functional throughout life (cf. Philobryidae).

From a theoretical perspective, reduction may affect any or all of the tooth series or subseries, as possibly in anomalodesmatans. Nonbrooding members of minorder Veneroitei show a tendency to suppress the entire G1 series, which in some taxa (e.g., *Chione* MEGERLE VON MÜHLFELD, 1811, and *Pitar* RÖMER, 1857) appears to be compensated by the earlier development of stronger interlocking hinge margins or cardinal tooth precursors in the larval shell. These cases of absence of the G1 or G2 tooth series are here viewed as convergent reductions, derived from the

ancestral bi-modular bauplan. This idea resurrects the question of convergence or homology of the G1-G2 pattern in Autobranchia and Protobranchia, which cannot be evaluated at present without speculating on the origin of the P-2 and G1a teeth series, and their relationship with the fordilloid early ontogenetic shell and its pretaxodont hinge. The first of two alternatives that must be considered is that the fordilloid or protobranch nepioconch is homologous with the P-2 of autobranchs; in this instance, the fordilloid pretaxodont teeth could have given rise to the protobranch G1 and autobranch G1 teeth series. The second is that the autobranch P-2 is an autapomorphy, in which instance the G1-G2 patterns of protobranchs and autobranchs appear to be convergent. At present, there is no convincing evidence of the evolution of fordilloid pretaxodont teeth into protobranch G1 or G2 teeth.

#### EARLY ONTOGENETIC SHELL TYPOLOGY

In a highly influential paper, OCKELMANN (1965) presented evidence for a correlation between egg size (yolk mass), developmental mode, and prodissoconch stages of marine bivalves (Table 1). His scheme soon became the standard reference for larval shells and the developmental modes inferred from them. However, it was not designed to address shell morphological diversity (OCKELMANN, 1965, p. 26) and is essentially restricted to marine autobranchs (see subsequent discussion of Yolk Mass and P-1 Paradoxes, p. 65, herein). Furthermore, the terminology does not allow for intermediate states, and it mingles concepts of morphology (P-1, P-2, size), energy source (planktotrophic, lecithotrophic), and location (planktonic, direct) that are not strictly correlated (see POULIN, VON BOLETZKY, & FERAL, 2001) and usually not testable in fossils (see section on Developmental Modes and subsequent sections, p. 59-73, herein). JABLONSKI and LUTZ (1983) provided a copious, concise review of classification schemes for marine invertebrate larvae. Intended to cover several marine invertebrate

TABLE 1. Correlation between developmental mode, yolk mass diameter (*y<sub>md</sub>*), and prodissoconch size (*P-1*, *P-2*) in marine autobranch bivalves (adapted from Ockelmann, 1965).

Developmental mode	<i>y<sub>md</sub></i> (μm)	<i>P-1</i> length (μm)	<i>P-2</i> length (μm)
planktotrophic, long pelagic cycle	40–85	70–150	<200–>600
lecithotrophic, short pelagic cycle	90–140	135–230	narrow to absent
lecithotrophic, direct development	150–>200	230–>1200	
		( <i>P-1</i> , <i>P-2</i> not specified)	

groups, their review, thus, only distinguished between planktotrophic and nonplanktotrophic larvae. A bivalve-specific approach was presented by HAIN and ARNAUD (1992), who found an apparent correlation between shell morphology and brooding type in various Antarctic species. However, their classification requires detailed anatomical knowledge of brooding types, which is presently unavailable for most species. In addition, their interpretation of shell stages (*P-1*, *P-2*), and thus measurements, are in disagreement with present usage (cf. LINSE & PAGE, 2003, p. 290).

We suggest herein an alternative classification scheme for early ontogenetic shell types, which is based solely on morphological criteria. It is noteworthy in this context that the shell-stage terms *P-1*, *P-2*, nepioconch, metaconch, and cryptoconch are also exclusively morphologically defined. Potential relationships between shell types and development will be addressed in the subsequent section.

**DESCRIPTIVE FRAMEWORK FOR EARLY ONTOGENETIC SHELL TYPOLOGY**

The present descriptive framework for shell typology uses a limited number of hierarchically nested morphological characters that, except for taxodont dentition in Protobranchia and hinge denticles, are all visible externally. At the primary level, ST-1 to ST-4 is used to distinguish between four main early shell types that are intended to encompass all bivalves. These primary types are further distinguished by secondary subtypes (A to D); the number of subtypes varies among the four primary shell types. At the tertiary level, shells are defined as either smooth (s) or

microsculptured (m) of the prodissoconch-1 or entire metaconch and cryptoconch, respectively. Because microstructural elements may be lost if the protective periostracum is eroded, shells should only be defined as smooth if this organic layer is present and smooth. A question mark (?) can be used to indicate equivocal or ambiguous instances; if both states occur in a species, polymorphism may be indicated by *s/m*. Finally, support characters, which refer to external and internal features, are used for easier distinction of main shell types and subtypes. Support characters are often convergent and not normally universally present in a group; therefore, they are not essential for any of the subdivisions.

All divisions are aimed at defining morphological grades. However, ST-1 and ST-4 also represent Protobranchia and Unionida, respectively. Note that type descriptions rely not only on qualitative, but also on quantitative characters that are often continuous in nature. As discussed below under Shell Type 2 (p. 53, herein), some overlap of subtypes and occasionally main shell types is unavoidable.

**SHELL TYPE 1**

**Definition**

Primary features of ST-1 (Shell Type 1) are the absence of a *P-2* stage in combination with a generally abrupt onset of the nepioconch. The nepioconch bears taxodont hinge teeth, except in solemyids. Support characters are the absence of a well-defined *P-1* cicatrix and metamorphic shell lip, a curved or (generally) poorly defined straight hinge line of the *P-1*, ellipsoidal (*L* > *H*), or indistinct roundish *P-1* outlines, a weakly opisthocline nepioconch, and nepioconch sculptures. The

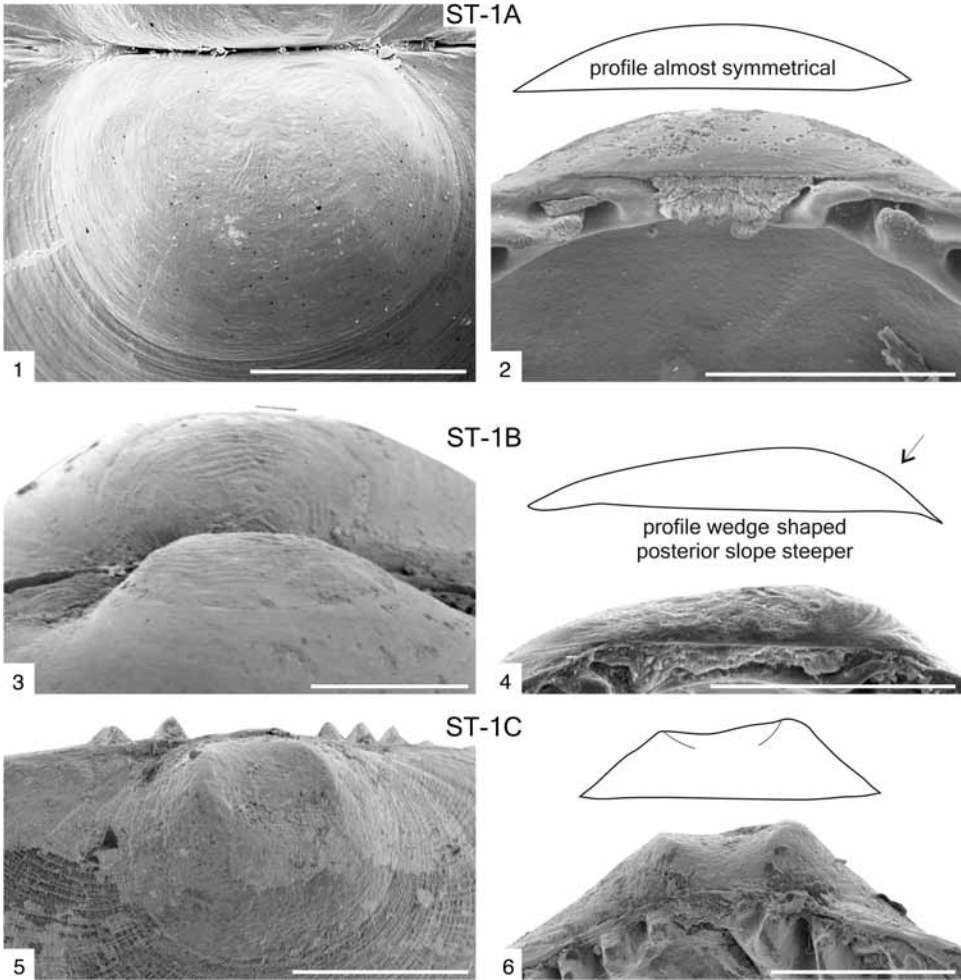


FIG. 33. Examples of early ontogenetic Shell Type 1 (Protobranchia). 1–2, ST-1A, *Yoldiella lucida* (LOVÉN, 1846) (A. Wáren, new); 3–4, ST-1B, *Nuculana pella* (LINNAEUS, 1758); 5–6, ST-1C, *Condylonucula bicornis* (GOFAS & SALAS, 1996); all specimens are RVs, scale bars, 100  $\mu$ m (new).

latter range from very fine commarginal growth—to commarginal ribs, antimarginally aligned irregular nodular sculptures, and continuous threadlike antimarginal microsculptures. Also, protobranchs lack shell tubules at all shell stages.

Secondary features are essentially based on morphological differences in the P-1 profile. ST-1A is defined by a homogeneously and nearly symmetrically convex P-1 profile, though a weak, apical depression may be present, as, for example, in some species of *Neilonella* DALL, 1881, and *Yoldiella* A. E.

VERRILL & BUSH, 1897 (see OCKELMANN & WÁRÉN, 1998; LA PERNA, 2007a).

ST-1B shells have a wedge-shaped profile. As far as currently known, the posterior slope is always steeper than the anterior, ramplike slope (apparently, most typical of Nuculidae and some Nuculanidae (Fig. 33.3–33.4) (e.g., GOFAS & SALAS, 1996; OCKELMANN & WÁRÉN, 1998).

ST-1C has a saddle-shaped profile with a deep central depression and a slightly steeper posterior than anterior slope (Fig. 33.5–33.6). This type is most characteristic

of *Condylonucula* D. R. MOORE, 1977, but see also *Nucula insignis* (HAYAMI & KASE, 1993) and *N. planiculmen* KILBURN, 1999. Transitional shapes may be described as ST-1A/B, 1B/C.

Tertiary features refer to smooth (suffix s) or microsculptured (suffix m) surfaces of the prodissoconch-1. Presently known ST-1 microsculptures include pitted, reticulate, commarginally corrugated, and corrugated-pitted. These sculptures may be genus- or species-specific in conjunction with other characters. The P-1 of solemyids appears to be smooth overall (but see discussion below).

### Discussion

Recent protobranchs never develop a prodissoconch-2; this is assumed to apply to the entire group. The fundamental difference between the protobranch ST-1 and morphologically similar autobranch type ST-2D (and to some degree also the autobranch ST-3A, 3C, as discussed below) is therefore primary absence versus (derived) reduction of a P-2 shell stage. This fact provides the main motivation for defining a separate (protobranch) shell type. It is important to note, however, that the morphological classification—based on the combination of primary and, where necessary, secondary shell features—should allow the distinction between protobranch and autobranch larval shells without the need for *a priori* assumptions in the majority of instances.

Solemyid larval shells are ambiguous because they are comparatively poorly known, and their postlarval shell stages are apparently edentulous at all growth stages. Outlines of *S. reidi* BERNARD, 1980, and *S. velum* SAY, 1822, are somewhat similar to the autobranch ST-3A. However, the P-1 lacks signs of a P-1/P-2 subdivision (cf. ST-3A), and the hinge line is not straight or it is only so for a very short distance; the shell surface is smooth to weakly corrugated commarginally (cf. GUSTAFSON & REID, 1986; GUSTAFSON & LUTZ, 1992).

The early shell of Cambrian *Pojetaia runnegari* JELL, 1980, is comparable to ST-1A,

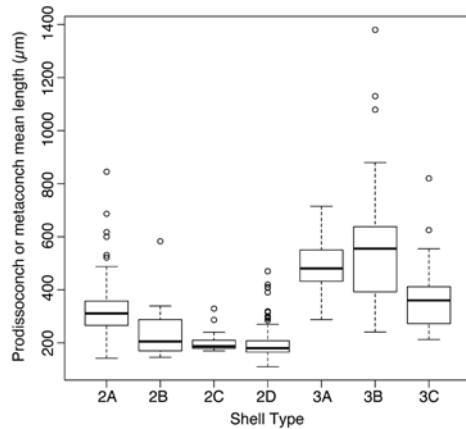


FIG. 34. Boxplot of P-2 or metaconch mean sizes in Autobranchia (excluding Unionida), grouped according to Shell Types 2A to 3C. Note the overall similarity of medians (around 200  $\mu\text{m}$ ) for ST-2B, 2C, and 2D. Number of observations: 2A = 131, 2B = 22, 2C = 30, 2D = 121, 3A = 11, 3B = 25, 3C = 31. Whiskers in these and subsequent boxplots show 1.5 IQR (interquartile range) (new).

with an ellipsoidal outline and apparently smooth surface. The distinct growth interruption within the second shell stage is also reminiscent of a similar growth line within the nepioconch of *Microgloma pusilla* (JEFFREYS, 1879) (cf. OCKELMANN & WARÉN, 1998). However, fordilloids (such as *P. runnegari*) lack protobranch taxodont hinge teeth and eubivalvian ligament characters.

### SHELL TYPE 2

#### Definition

Primary features are well-defined prodissoconch stages 1 and 2 (ST-2A, 2B, 2C), or the (nearly) complete reduction of the P-2 (ST-2D). Overall, prodissoconch profiles are homogeneously convex to inflated, sometimes inequilateral. Larval shells lack tubules. This type includes the majority of autobranchs.

Secondary features are based on ranges of the P-1/P-2 length-ratio (Fig. 34; see discussion for rationale). ST-2A and ST-2B have a small- to medium-sized P-1 ( $\sim 50\text{--}200\ \mu\text{m}$ , often below  $100\ \mu\text{m}$ ), a large P-2, and differ in the length ratio. ST-2A is characterized by ratios below 0.5 (Fig. 35.1–35.2), whereas

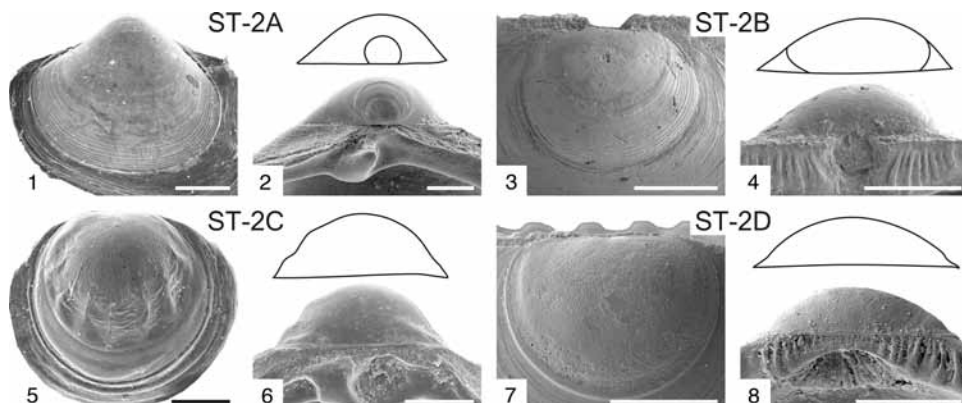


FIG. 35. Examples of early ontogenetic Shell Type 2 (marine Autobranchia), scale bars, 100  $\mu\text{m}$ . 1–2, ST-2A, *Hiatella arctica* (LINNAEUS, 1767 in 1766–1767), LV, RV (new); 3–4, ST-2B, *Glycymeris violacescens* (LAMARCK, 1819 in 1818–1822), LV, RV (Malchus & Warén, new); 5–6, ST-2C, *Cardita calyculata* (LINNAEUS, 1758), RVs; 7–8, ST-2D, *Crenella magellanica* LINSE, 2002, LVs (Malchus & Linse, new).

ST-2B displays ratios between 0.5 and 0.75 (Fig. 35.3–35.4).

Support characters for ST-2A and ST-2B are regular commarginal growth lines or welts of the P-2; well-developed antimarginal threads are known only in *Dreissena* VAN BENEDEEN, 1835 (see ZARDUS & MARTEL, 2006, fig. 15.14C–D); beaks pointed and projecting beyond the straight hinge line (in ST-2B less than in ST-2A); and advanced P-2 shells usually with well-developed G1a teeth and a ligament (mineralized or not). ST-2A is possibly the most common early ontogenetic shell type among marine bivalves (cf. Fig. 1, Fig. 7.1, Fig. 13, Fig. 17.1–17.2).

ST-2C has a medium- to large-sized P-1 (~120–260  $\mu\text{m}$ ), a small P-2, and P-1/P-2 length ratios above 0.75 and up to 0.95 (Fig. 14.1, Fig. 35.5–35.6). A support character is an inflated P-1, giving the shell a knobby or dome-like appearance; this P-1 does not project beyond the hinge. The P-2 usually grows nearly horizontally and forms a marked angle with the inflated P-1. Note that the P-1/P-2 ratio only reflects little P-2 growth in length, whereas ventral growth is often more substantial (hence, length and height ratios are not equivalent). Species with ST-2C (sometimes 2C/2D) shells are found in Pectinidae (WALLER, 1993; DIJKSTRA & GOFAS, 2004), Recent and fossil Astartidae

(*Goodallia* TURTON, 1822; *Nicaniella* CHAVAN, 1945; *Oxyeurax* GARDNER & CAMPBELL, 2007) (GIRIBET & PEÑAS, 1999; this study), or Cuninae (MIDDELFART, 2002b), among others.

ST-2D may develop a considerably larger P-1 than the previous ST-2 subtypes (up to 540  $\mu\text{m}$ , possibly 750  $\mu\text{m}$ ), and the P-2 is absent or reduced to a concave or swollen narrow rim (P-1/P-2 length ratios above 0.95). The P-2 rim, if present at all, shows similar widths around the P-1 (Fig. 35.7–Fig. 35.8; it may represent a smooth metamorphic lip or consist of a few growth lines (Fig. 14.2). Larger 2D shells tend to become slightly inequilateral and D-shaped and, thus, transitional to ST-3B (cf. Fig. 37.3); or they become weakly raised above the postlarval shell and may then be transitional toward ST-3C; as, for example, in some species of *Barbatia* GRAY, 1842 (see OLIVER & HOLMES, 2004, fig. 27–29). Species with typical ST-2D are found in Limopsidae and Crenellidae (OCKELMANN, 1983; SALAS & GOFAS, 1997; MALCHUS & WARÉN, 2005); the P-1 of Cuninae (Condylocardiidae) often ends in a thick shell rim (MIDDELFART, 2002b).

In both ST-2C and ST-2D, but more typically in the latter subtype, the P-1 may lack a cicatrix, as in some Limopsidae and Crenellinae. Hinge teeth and ligament are

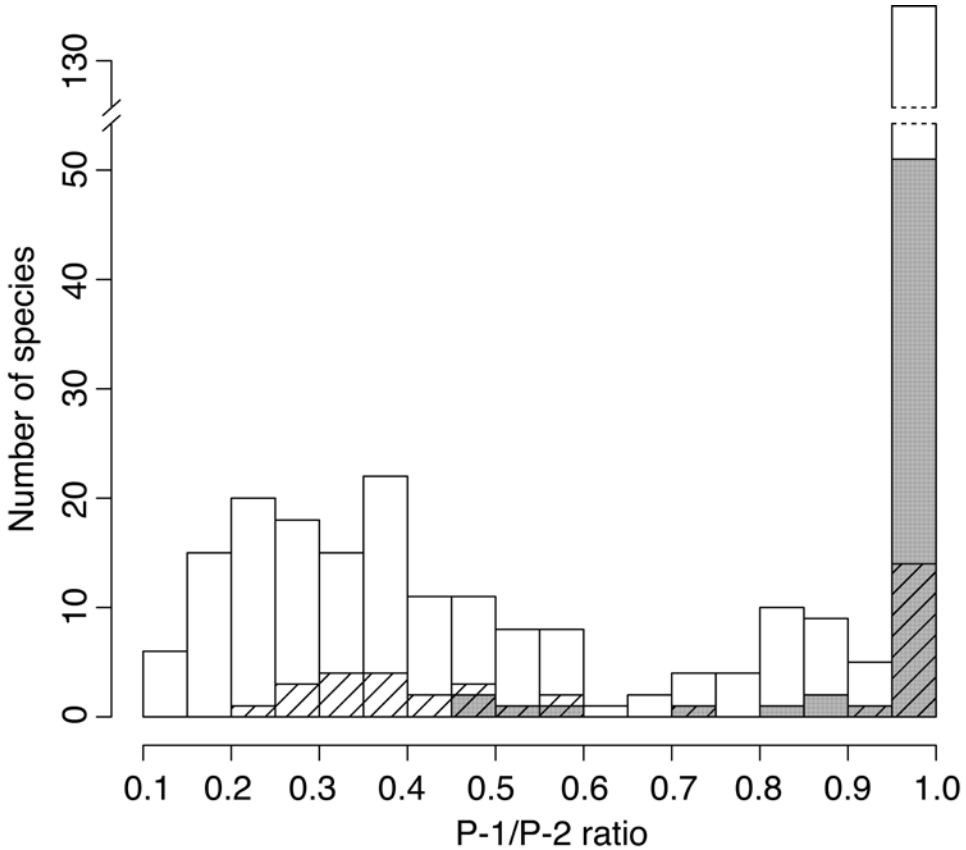


FIG. 36. Frequency histogram showing the distribution of P-1/P-2 ratios in bivalves. Ranges 0.1 to 0.5 correspond to ST-2A; 0.5 to 0.75 to ST-2B; 0.75 to 0.95 to ST-2C; and 0.95 to 1 to ST-2D. Grey bars indicate shells with P-1 length  $\geq 200 \mu\text{m}$ ; cross-hatched bars indicate species for which direct evidence of brooding is available (new).

either absent or poorly developed prior to the nepioconch stage.

As tertiary features, sculptured surfaces of ST-2 P-1 are usually pitted, sometimes also with antimarginal elements, whereas commarginal corrugations or reticulate patterns have not been observed. In addition, Cuninae and the astartid genus *Goodallia* tend to develop marginal indentations on their P-1. The rather crumbled P-1 surface of some *Warrana* species (Cuninae), resembling a “deflated balloon” (MIDDELFART, 2002b, p. 94), seems to represent an extreme development of such marginal indentations.

### Discussion

ST-2D morphologically approaches the protobranch ST-1A and 1B. However, the hinge line of ST-2D is straight and long, the profile usually nearly equilateral, and the outline more circular. In addition, the early postlarval hinge tooth shape, size, and arrangement differ from ST-1 teeth. P-1 plus nepioconch never appear to be opisthocline; this observation requires confirmation, however.

BERKMAN, WALLER, and ALEXANDER (1991) suggested the use of length ratios as a complementary measure to absolute P-1

dimensions in order to distinguish shells derived from planktotrophic development (ratio < 0.4) and those indicating lecithotrophic development (ratio > 0.6). Available evidence indicates a decline in the frequency of occurrences around 0.6 to 0.7, rather than a gap between 0.4 to 0.6 (Fig. 36), which seems to imply some kind of bimodal distribution. However, the decline does not mark the difference between pure planktotrophic and pure nonplanktotrophic development as was intended by BERKMAN, WALLER, and ALEXANDER (1991). For example, species with P-1 sizes larger than or equal to 200  $\mu\text{m}$ , indicating lecithotrophic eggs, may also have a large P-2 and thus P-1/P-2 ratios below or around 0.4, suggestive of an extended period of planktotrophy (e.g., *Pulvinites* DEFRANCE, 1824; *Divariscintilla* POWELL, 1932; MIKKELSEN & BIELER, 1989, 1992; TEMKIN, 2006; see also section on Inferring Endotrophy and Exotrophy, p. 62, herein). Given the bewildering variety of developmental modes displayed by bivalves (see below), it does not seem possible to identify universally indicative ranges of the ratio. The values of 0.5, 0.75, and 0.95, arbitrarily defined as thresholds between subtypes of ST-2 in the present approach, are those that seem to empirically correlate with other morphological characters used in the definitions of subtypes; alone, they are not reliable indicators of developmental modes.

In this study, we have roughly estimated the range of P-1/P-2 ratios of species by calculating P-1min/P-2max (lowermost ratio) and P-1max/P-2min (highest ratio). This rule-of-thumb method is likely to overestimate the range of a sample, but it may also partially compensate for the fact that size data for larval shells are frequently based on small sample sizes. Ratio ranges calculated by this method from published data have usually proved reasonable, including those indicating overlap of two adjacent shell types. Overall, the upper-range limit rarely becomes greater than one. Note that the P-1 length cannot be larger than the sum of the individual lengths of P-1 and P-2. The

method is not applicable to ST-2D, because it may lead to unrealistic ratio ranges below 0.95 and above 1. Results indicating a range across three subtypes are usually based on indirect measurements (i.e., the scale bar of a published image), thus introducing additional error, or on ambiguous interpretations of P-1, P-2, and nepioconch boundaries (see also ST-3, below). Hence, overlap involving two subtypes arguably reflects true variance of a sample or species, whereas larger ranges are more likely artifacts due to vague boundary definitions or scaling.

### SHELL TYPE 3

#### Definition

Primary features of ST-3 are poorly marked P-1 and P-2 growth stages (although P-2 may be large) and potentially a welded nepioconch (hence, cryptoconch and metaconch). Profiles are generally distinct from ST-2 (see description of subtypes below). Most shells possess a marked cicatrix, which may be very weakly to deeply dented. For size ranges, see Figure 34.

ST-3A has a rather flat to moderately and homogeneously convex profile; P-2 growth lines are fine to nearly obsolete; the margin toward the nepioconch is distinct but not steplike. Most of these shells have equilateral ellipsoidal ( $L > H$ ) to obliquely and inequilateral ellipsoidal outlines, and some show incipiently developed ears (Fig. 10.1). Overall, ST-3A shells lack sculpture (but see tertiary features). Examples are found among species of *Ostrea* LINNAEUS, 1758, and *Lasaea* T. BROWN, 1827 (Fig. 37.1–37.2; CHANLEY & DINAMANI, 1980; Ó FOIGHIL, 1986, 1989; Ó FOIGHIL & THIRIOT-QUIÉVREUX 1999).

ST-3B is a metaconch/cryptoconch with an overall flat, ragged, or somewhat domed central profile; the outline is usually inequilateral D-shaped. It is clearly set off from the subsequent shell by a small steplike to high and steep flank. Examples include numerous arcoids (e.g., Philobryidae, *Barbatia* GRAY, 1842); Cyclochlamydidae (*Cyclochlamys* FINLAY, 1926, right valves);



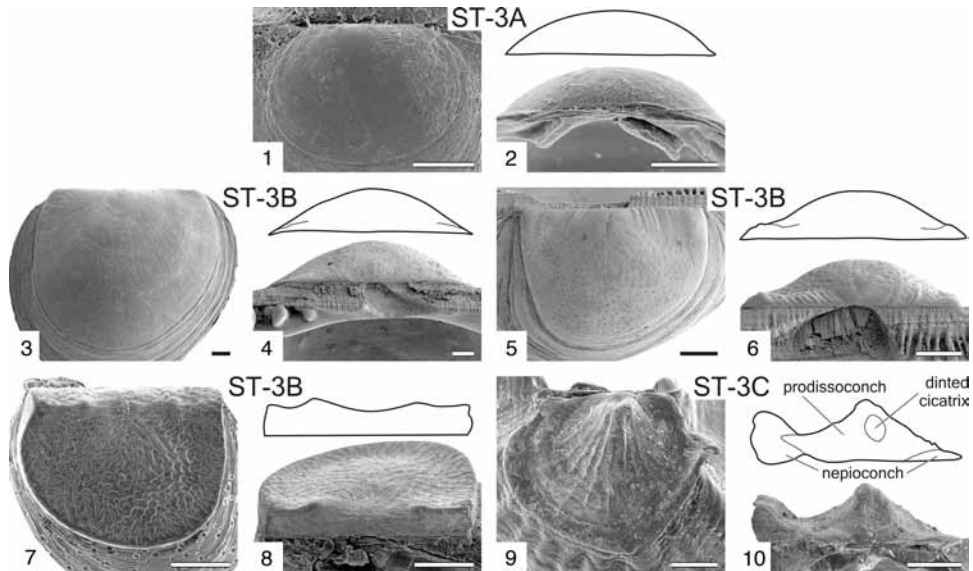


FIG. 37. Examples of early ontogenetic Shell Type 3 (marine Autobranchia), scale bars, 100  $\mu$ m; 1–2, ST-3A, *Lasaea colmani* Ó FOIGHIL & THIRIOT-QUIEVREUX, 1999, LV, RV; 3–8, ST-3B, *Lissarca notorcadensis* MELVILL & STANDEN, 1907, RVs; *Philobrya wandelensis* LAMY, 1906, RV, LV; *P. meleagrina* (BERNARD, 1896c), RVs; 9–10, ST-3C *Condylocardia hippopus* (MÖRCH, 1861 in 1859–1861), LVs (new).

and Condylocardiidae (*Austrocardiella* MIDDELFART, 2002a; *Benthocardiella* POWELL, 1930), among others (Fig. 37.3–37.8; DELL, 1964, 1990; MIDDELFART, 2002a; OLIVER & HOLMES, 2004; MALCHUS, 2006). CHAPARRO and others (2011) illustrated a cryptoconch (probably P-1) of *Gaimardia bahamondei* OSORIO & ARNAUD, 1984, which represents a transitional shell type between ST-2D (overall outline) and ST-3B (domed central portion with distinct microsculpture and differentiation of ears). It is currently coded as ST-3B.

ST-3C is characterized by a distinctly conical profile (often with a dented apex); shells are often raised above the subsequent shell and separated from it by a steep or undercut flank (Fig. 15.2–15.4). Shells may be metaconchs or cryptoconchs (e.g., Pectinoidea: left valves of species of *Cycloclamys* FINLAY, 1926, and *Cyclopecten* A. E. VERRILL, 1897; some arcoids: *Barbatia* GRAY, 1842, *Cratis* HEDLEY, 1915, *Cosa* FINLAY, 1926; and numerous Condylocardiinae (see SALAS & ROLÁN, 1990; SALAS & COSEL, 1991; HAYAMI & KASE 1993; MIDDELFART, 2002a; MORAN,

2004a; OLIVER & HOLMES, 2004; DIJKSTRA & MAESTRATI, 2012) (Fig. 37.9–37.10). Many Condylocardiinae have transitional ST-3B/3C features.

Support characters for many ST-3B and 3C shells are inequilateral, D-shaped outlines, and thickened dorsal shoulders or ears, which are rarely separated by a notch from the main shell disk (e.g., *Cyclopecten* A. E. VERRILL, 1897; HAYAMI & KASE, 1993, fig. 211; OLIVER & HOLMES, 2004, fig. 64–65). Shell flanges that produce undercutting typically belong to the nepioconch (Fig. 6.3–6.4). Tertiary, microsculptural features of ST-3A are either a smooth or a pitted P-1. For the other subtypes, microsculpture refers to the entire metaconch/cryptoconch and is, overall, highly diverse, complex, and often species specific within the same higher taxon. Shells are considered smooth (s) if this is the overall condition, excluding cicatrix wrinkles, fine commarginal lines, and also subdued antimarginals as are common in ST-3A (e.g., *Lasaea* T. BROWN, 1827, in Fig. 10) and some ST-3B (Fig. 37.3). Such

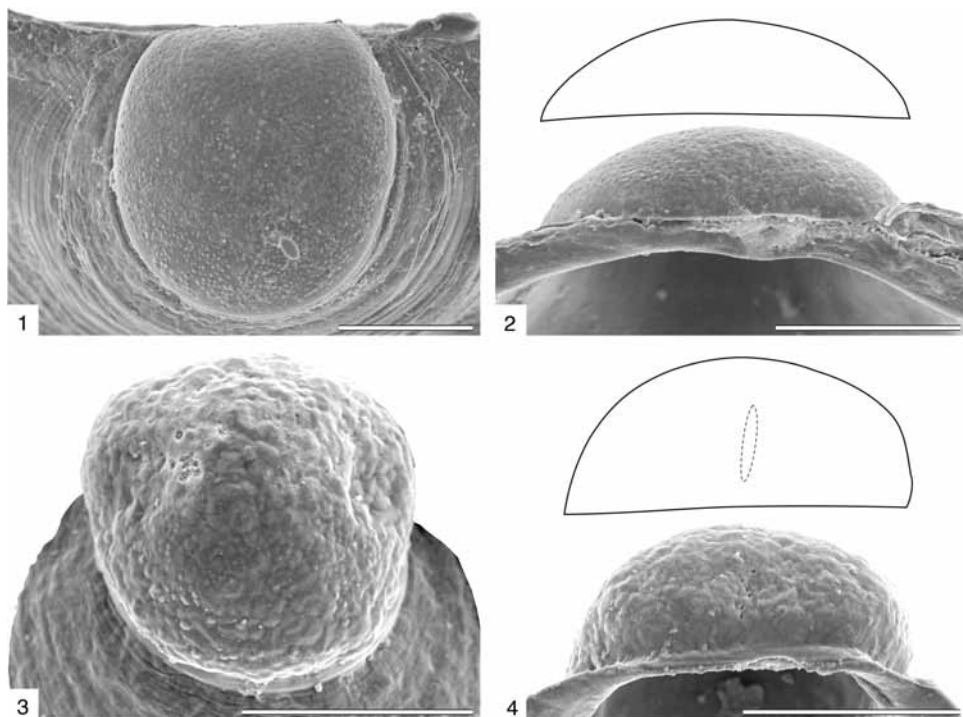


FIG. 38. Examples of early ontogenetic Shell Type 4 (order Unionida) of excysted glochidial shells with early nepioconchs, scale bars, 100  $\mu\text{m}$ ; 1–2, *Potomida littoralis* (CUVIER, 1798), LV, RV; 3–4, *Margaritifera auricularia* (SPENGLER, 1793), LV, RV (SEM specimens cultured by M.-A. López; Malchus & López, new).

subdued structures may be referred to separately in a taxonomic description. All other (generally coarser) surface microstructures are collectively coded as microsculpture (m) (Fig. 15.2–15.4, Fig. 16.1).

#### SHELL TYPE 4

##### Definition

Primary features (ST-4): Shells are either cryptoconchs, possibly including a P-2 in many cases (the development of a nepioconch before encystment is questionable), or organic, noncalcified mono-valves (lasidia, haustoria). Most mineralized shells (glochidia) possess some type of fine to roughened, pustular/pitted, ribbed or vermiculate external, and fine, pustular internal surface microsculpture. Most taxa also possess shell tubules (reduced or absent in Margaritiferidae), small, marginal shell microdenticles (micropoints) and/or a few

shell hooks (rarely more than one), which may be armored with styli-form dents. The postlarval shell lacks tubules. Secondary and tertiary features are presently not defined. Mineralized glochidial shells represent the most common ST-4 (Fig. 38.1–38.4; cf. Fig. 11, Fig. 17.3,5, Fig. 18).

##### Discussion

Unionid workers have developed their own terminology for larval types (glochidium, lasidium, and haustorium) and glochidial shell characters (e.g., CLARKE, 1981, 1985; HOGGARTH, 1999, table 1; GRAF & CUMMINGS, 2006, p. 360). Therefore, we do not define any shell subtypes.

Nevertheless, we note the following potential distinctions based on the timing of completion of shell development and growth mode: (a) shells that are uncalcified at release from the mother and whose valves must

therefore undergo biomineralization during the parasitic phase (lasidium, haustorium); (b) bivalved glochidia that continue to significantly increase in size during the parasitic phase (e.g., *Margaritifera*, and some *Lampsilini*); (c) shells that undergo remodeling, at this time confirmed only for *M. auricularia* (SPENGLER, 1793); and (d) shells that do not grow significantly during the parasitic phase—that is, shells that are essentially fully grown at release from the mother (apparently the majority of glochidia).

Although the current literature does not provide any systematic approach for comparing shell development in unionids and marine bivalves, glochidia show two or three shell stages. First is the densely microsculptured stage, which may have cicatrix-like corrugations at the umbo; second is a smooth stage, which may be absent to very large; and third is a stage that is often rather narrow, with commarginal growth lines. These stages are somewhat reminiscent of P-1, P-2, and the metamorphic shell lip or nepioconch of marine bivalves. It also appears that denticles, hooks, and thickened dorsal shell margins (alae) develop during the second, or perhaps third, stage.

Another point of comparison is shell size. All unionoid species belonging to categories (b) and (c) produce small-shelled glochidia (~50–150  $\mu\text{m}$ ) lacking hooks. By contrast, the overwhelming majority of glochidia in category (d) are ~180–380  $\mu\text{m}$  in size and hooked (cf. CLARKE, 1981, 1985; BAUER, 1994; PEKKARINEN & ENGLUND, 1995a; HOGGARTH, 1999). These size categories are roughly comparable to marine bivalve larvae with a small- to medium-sized P-1 (~50–200  $\mu\text{m}$ ), mostly categories ST-2A–D, and to shells with a large P-1 or metaconch/cryptoconch type shell (mostly ST-3), respectively. Future studies may reveal to what extent these similarities are based on homologous growth patterns.

## DEVELOPMENTAL MODES

Larval development of bivalves has been described or reviewed by THORSON (1946,

1950), OCKELMANN (1965), SELLMER (1967), ANDREWS (1979), SASTRY (1979), KASYANOV and others (1983, 1998), MACKIE (1984), and SAUCEDO and SOUTHGATE (2008). In addition, it has been described or reviewed in earlier works by LACAZE-DUTHIERS (1854), PELSENEER (1903, 1920, 1935), and LEFEVRE and CURTIS (1910, on unionoids), among others. BENINGER and LE PENNEC (1997) compiled data on bivalve egg diameters, and GUSTAFSON and REID (1986) on egg, prodissoconch, and adult shell sizes in protobranchs. The data indicate an extraordinary repertoire of developmental modes in which energy source and quantity, developmental site, and developmental timing are arguably among the most relevant variables.

Energy source includes planktotrophy, lecithotrophy, parasitism (host-feeding), matrotrophy, and combinations thereof. Larval parasitism is only known in unionoids within the Bivalvia, but matrotrophy occurs in virtually all freshwater bivalves (unionoids, sphaeriids, cyrenids) and in Teredinidae (e.g., CALLOWAY, 1982; DURFORT, 1985; GRAF & Ó FOIGHIL, 2000; SCHWARTZ & DIMOCK, 2001; KORNIUSHIN & GLAUBRECHT, 2003, 2006; GLAUBRECHT, FEHÉR, & VON RINTELEN, 2006; CRAGG & others, 2009; SHIPWAY, 2012), whereas the presence of nurse cells still needs confirmation (MACKIE, 1984, p. 382).

Numerous bivalves combine various energy sources that give rise to a considerable overlap in planktotrophic and lecithotrophic egg sizes. However, this does not apply to Protobranchia, which are all assumed to be lecithotrophic (ALLEN & SANDERS, 1973); the same is probably also true of Unionida (BAUER, 1994; PEKKARINEN & ENGLUND, 1995a; ARAUJO & RAMOS, 1998).

The site of development may be almost any combination of planktonic, demersal, and brood protected. Brooding itself comprises a variable set of external and internal modes. External brooding includes the formation of a brood sac attached to the shell or byssus of the female (DREW, 1899, in *Nucula* LAMARCK, 1799; OLDFIELD, 1955, in *Turtonia* ALDER, 1848), nest

TABLE 2. General trends in Autobranchia shell, egg, and brooding characters. Egg sizes are assumed yolk mass diameters. Measurements in  $\mu\text{m}$ . Question marks indicate that a mode is unknown for one or more species. Shell types followed by (all) include all species with this shell type, while (br) indicates brooding species; all species with Shell Types 3A to 3C are brooders. Asterisks (\*) indicate that the egg size is based on a single species or specimen; *av*, advanced veliger; *bc*, brood chamber; *bn*, byssus nest; *bs*, brood sac; *ct*, ctenidial; *ctp*, ctenidial brood pouch; *dv*, D-veliger; *es*, egg string; *j*, juvenile; *jc*, jelly coat; *mc*, mantle cavity; *O*, oviparous; *Ob,jc*, oviparous-benthic with jelly coat; *O,jc*, oviparous with jelly coat; *sct*, supractenidial; *sd*, shell depression; *tr*, trochophore; *vt*, ventilation tube (new).

Shell Type	Egg size	P-1 length	Overall length	Internal brooding	External brooding	Release
2A (all)	25–90	40–190	140–620	—	—	O, O,jc
2A (br)	40–90	76–155	190–580	ct, sct	?	dv, av
2B (all)	60–170	62–299	130–616	—	—	O,jc (dv), ?
2B (br)	100–170	142–299	260–616	ct, mc, jc	?	dv
2C (all)	92–580	104–591	166–750	—	—	O,jc, O,jc (tr, dv)
2C (br)	500–580*	164–591	177–750	ctp, ?	?	j, ?
2D (all)	80–190	110–540	110–540	—	—	O,jc, Ob,jc
2D (br)	125–155	150–442	150–442	bc, ct, ctp, mc, sd	bn, bs, jc, es, vt, sd	av, j
3A	158–300	—	288–715	ct, mc, sct	bs	av, j
3B	327–464*	—	211–1380	mc	?	j, av
3C	206–223*	—	197–820	mc, sct, ?sd	?	j, av

building as in various mytilids and possibly limids (THORSON, 1946; MINER, 1950, *vide* SELLMER, 1967; MERRILL & TURNER, 1963; see also MIKKELSEN, 2011: *Limatula*), retention in ventilation tubes within the sediment [e.g., *Crenella decussata* (MONTAGU, 1808), G. E. DINESEN, personal communication, 2005], or deposition of egg strings (THORSON, 1935). In some bivalves, larvae develop from negatively buoyant, demersal eggs, individually encased by a gelatinous and sticky egg capsule: *Laternula elliptica* (KING & BRODERIP, 1832); PECK, POWELL, and TYLER, 2007; see further examples below.

Internal brooding may occur between ctenidia (with or without brood pouches or water tubes), lying free in the ventral or dorsal mantle chamber, individually attached to the mantle, or in special brood pouches (MACKIE, 1984; HAIN & ARNAUD, 1992; KORNIUSHIN, 2000; PASSOS & DOMANESCHI, 2009; among many others). In *Gaimardia bahamondei* OSORIO & ARNAUD, 1984, each embryo is surrounded by an individual envelope anchored by a peduncle to the abfrontal region of the ctenidial filaments. In the final brooding stage, the embryos become detached and fall into the ventral region of the supra-branchial chamber, before being expelled via

the excurrent jet (CHAPARRO & others, 2011). For modified ctenidial systems in unionoids, see GRAF and Ó FOIGHIL (2000).

Timing in the present context refers to the duration of internal brood protection. Broadcast spawning (brooding duration of zero) is apparently the most common mode among marine bivalves (LOOSANOFF, DAVIS, & CHANLEY, 1966; CHANLEY & ANDREWS, 1971; LE PENNEC, 1978; KASYANOV & others, 1983, 1998; SAUCEDO & SOUTHGATE, 2008, among many others). However, there is an increasing number of records of species with egg retention (brooded to early shelled stages; usually D-veliger in autobranchs), release of nearly competent larvae, or birth of postlarvae (direct development) (for example, DALL, 1903b; YONGE, 1969; OCKELMANN & MUUS, 1978; MIKKELSEN & BIELER, 1989, 1992; SALAS & COSEL, 1991; SCHNEIDER, 1993; SALAS & GOFAS, 1997, 1998; Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999; MIDDELFART, 2002a, 2002b; PASSOS & DOMANESCHI, 2009; SHIPWAY, 2012; see also references in the section Developmental Modes, p. 59, herein) (Tables 2–13). SELLMER (1967) and GLAUBRECHT, FEHÉR, and VON RINTELEN (2006) discussed the related terminology: ovoviviparity, larviparity, direct development, euviviparity, and matrotrophy.

TABLE 3. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorphia: Mytilida: Mytiloidea (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Subsequent cells (of a line) summarize data from different species; *P-1 length*, prodissoconch-1 length. Blank cells indicate knowledge gaps. Measurements are in  $\mu\text{m}$ ; measurements in brackets are considered dubious; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. Early ontogenetic shell type: *2A*, *3C*, main shell types; *2A/2B* (and similar), transitional types. Genera: *F*, fossil taxon. Principal modes: *E.dw*, dwarf males attached to exterior of female; *EB*, external brood protection; *EB.bn*, byssus nest; *EB.bs*, brood sac; *EB.bs.jc*, jelly-coated eggs in brood sac; *EB.es*, egg string; *EB.vt*, ventilation tube; *IB*, internal brooding; *IB.bc*, brood chamber; *IB.ct*, ctenidial; *IB.ctp*, ctenidial brood pouch; *IB.dw*, internally attached dwarf males; *IB.jc*, jelly-coated egg; *IB.mc*, mantle cavity; *IB.sct*, supracatenidial; *jc*, jelly coat; *O*, oviparous; *O.jc*, oviparous with jelly coat; *Ob*, oviparous-benthic; *Ob.jc*, oviparous-benthic with jelly coat; *Op*, oviparous-pelagic; *Op.jc*, oviparous-pelagic with jelly coat. Release types: *av*, advanced veliger; *dv*, D-veliger; *j*, juvenile; *tr*, trochophore (only in one *Pandora*) (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Mytiloidea					
<i>Bathymodiolus</i>	57–80	103–116	430–455	Op	2A
<i>Amygdalum</i>	60–70		400		
<i>Limnoperna</i> (2)	45–50	<80	289–330	Op, ?	2A
<i>Modiolus</i> (6)	55–81	95–122	220–485	O, Op, ?	2A
<i>Musculus</i> (4)	150–440	300–540	300–540	EB.bn, EB.es, ?IB	2D, 2D/3A
<i>Mytilus</i> (2)	70	90	210–260	Op	2A
<i>Perna</i>		75–91	300–400	Op	2A
<i>Rhomboidella</i>	80	122–131	122–131		2D
<i>Rhomboidella</i> (2)		315–329	315–329		2D
<i>Crenella</i> (2–3)	125–>155	140–210 [290]	140–210 [290]	EB.vt, ?	2D
<i>Dacrydium</i> (9)	95–115	160–204	160–204	IB.bc, ?	2D
<i>Dacrydium</i> (3)			210–315	IB, IB.mc	2D/3B

Other endogenic variables that may influence early ontogeny are the difference in the larval bauplan (pericalymma, veliger), yolk quality as suggested by small lecithotrophic eggs in some Protobranchia, oocyte membranes and gelatinous coat (THORSON, 1946; FRENKIEL & MOUÉZA, 1979; GROS, FRENKIEL, & MOUÉZA, 1997; MOUÉZA, GROS, & FRENKIEL, 1999, 2006; COLLIN & GIRIBET, 2010), and anatomical constraints of the adult. For example, ctenidial brooding seems to occur preferentially in eulamellibranch and pseudoeulamellibranch (ostreoid) bivalves. OCKELMANN (1965, p. 27) noted that egg size may be related to adult size. It also appears obvious that egg size, larval size, and number of brooded larvae are

constrained by the available brood space. Hence, offspring number may range from a single to several hundred thousand specimens (HILL & KOFOID, 1927, p. 284; HAIN & ARNAUD, 1992; OCKELMANN & WARÉN, 1998; CRAGG & others, 2009).

Developmental modes and the different types of larval shells evolved within this multidimensional space of interrelated variables. Unfortunately, adequate multivariate or factorial analyses are hampered by datasets that are too incomplete and heterogeneous. The most fundamental difficulties concern the comparability of egg-size measurements and shell stages and a lack of detailed observations on internal brooding types. Gametogenetic studies tend to measure

TABLE 4. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorpha: Arcida: Arcoidea (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Arcoidea					
<i>Acar</i> (4)	150–223		230–410	IB.mc, IB.?:bp (j)	3C
<i>Acar</i>		170–196	170–196		2D
<i>Anadara</i>	52	70–85	220–260	Op	2A
<i>Arca</i>		173–183	173–183		2D
<i>Asperarca</i> (3)			211–330		3B/3C, 2D/3C
<i>Barbatia</i> (3)		180–192	180–192		2D
<i>Barbatia</i> (2)			276–560		3B
<i>Calloarca</i>			420		3B
<i>Mimarcaria</i> (2)			283–313		3B
<i>Xenophorarca</i> (2)		101–151	174–340		2B, 2D/3B
<i>Striarca</i> (1–2)		89–122	177–201		2A, 2B/2A
<i>Striarca</i> (F)		60	250		2A
<i>Grammatodon</i> (1–2) (F)		68–105	215–291		2A
<i>Limopsis</i> (7)	135–140	170–200	170–200		2D
<i>Limopsis</i> (4)		230–540	230–540		2D, 2D/3C
<i>Adacnarca</i>			226–255		3B
<i>Adacnarca</i> (2)	380		372–588	IB.mc (av, ?j)	3B
<i>Adacnarca</i>		-280	880	IB	?
<i>Cosa</i> (4)			197–308	IB (av, j)	3C
<i>Cosa</i> (F)			640		3B
<i>Cratis</i> (3)			230, 250–596		3C, 2D/3B
<i>Limarca</i> (F)			500–750		3C
<i>Lissarca</i> (2)			609–1200	IB	3B
<i>Philobrya</i> (6)			349–800	IB, IB.mc, (j)	3B

egg surface and mean diameter within the gonads from which a theoretical oocyte diameter can be calculated [square root of  $(4A/\pi)$ , where  $A$  = surface area], and it is not always clear whether these refer to ripe eggs. Other sources report diameters for shed eggs or yolk mass diameter (ymd), which are not necessarily the same; however, ymd, not egg diameter, was used by OCKELMANN (1965) as a proxy to distinguish between planktotrophic and lecithotrophic development. Embryological studies rarely provide images or descriptions of the larval shell, and varying concepts of shell stages P-1, P-2, and nepioconch among studies compromise the comparability of both shell types and dimensions. Finally, while results from HAIN and

ARNAUD (1992) suggest that different kinds of internal brooding may influence the shell type, sufficiently detailed descriptions are uncommon and usually lack data on the early ontogenetic shell (but see CHAPARRO & others, 2011, on *Gaimardia bahamondia* OSORIO & ARNAUD, 1984).

## INFERRING ENDOTROPHY AND EXOTROPHY

This section briefly outlines presumptions and current limitations for inferences of larval trophic requirements from egg and prodissoconch-1 sizes. It also explores relationships between these variables and Shell Types 2A to 2D, which are not self-evident,

TABLE 5. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorphia: Pectinida (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Dimyoidea					
<i>Atreta</i> sp. (F)		82–89	170–184		2A
Oxytomoidea					
<i>Meleagrinella</i> sp. (F)		86	383–425		2A
<i>Oxytoma</i> (2) (F)		56–80	232–310		2A
Pectinoidea					
Pectinoid? M9 (F)		65	300		2A
<i>Camptochlamys</i> sp. (F)		64–73	231–246		2A
<i>Adamussium</i>	45–65	110–145	303–403	Op	2A
<i>Aequipecten</i> (2)		81–95	216–231	O, Op	2A
<i>Caribachlamys</i> (3)		104–163	175–179		2C
<i>Chlamys</i> (2)	70–90	105	220–280		2A
<i>Crassadoma</i>		92	200		2A
<i>Hyalopecten</i>		218	218		2D
<i>Mimachlamys</i>	65	90	210	Op	2A
<i>Palliolum</i>		81–87	225		2A
<i>Pecten</i>	70	80	300	Op	2A
<i>Pseudamussium</i> (2)		100–125	320–340		2A
<i>Pseudobinnites</i>	170–180	230–260	230–260		2D
<i>Talochlamys</i> (2)					
Entolioidea		88–133	196–200		2A, 2A/2B
<i>Cyclochlamys</i> (3)			246–330	IB.ct, IB.sct (j), ?	3C, 2D/3B
<i>Cyclopecten</i> (3)	105–130	~130	164–220		2D, 2B/2D?, ?
<i>Parvamussium</i> (5)		140–204	140–204		2D
<i>Propeamussium</i> (8)	110–180	200–290	200–290		2D, ?

given that the shell typology was developed independently of any assumption on energy sources and developmental modes.

Endotrophy here refers to lecithotrophy; extotrophy includes planktotrophy (most common), matrotrophy, and host-feeding. Other energy sources are presently unknown for bivalve larvae. Graphics and statistical analyses in this and the following sections are drawn from a compilation of data from the literature sources cited above, as well as from our own observations (Table 14). See BAUER (1994), MORAN (2004b), and J. T. SMITH (2007) for additional data on unionids, arcids, and pectinids, respectively.

The most complete parameters are shell size and shell type, available for >80% of the species in the dataset. Only direct evidence of developmental modes was taken into consideration. This procedure, which drastically reduced sample size, seemed necessary to avoid circular reasoning.

Prodissoconch sculptures and nepioconch features were not considered in the statistical analysis, because data on these features are still too scanty to provide meaningful interpretation. For similar reasons, Euprotobranchia, Trigoniida, and Unionida had to be excluded. However, these taxa are still referred to in the text and tables.

TABLE 6. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorpha: Limida (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
<i>Ctenoides</i> (6)		160–240	160–240		2D
<i>Divarilima</i>		~165	200–226		2C
<i>Lima</i> (2)		195–300	195–300		2D
<i>Limaria</i> (3)		76–114	258–347		2A
<i>Limaria</i>		160	160		2D
<i>Limatula</i>			410		2A
<i>Limatula</i> (9)	130	110–200	110–200		2D
<i>Limatula</i> (4)	150	200–420	200–420	IB.ctp, ?IB.mc	2D
<i>Limatula</i>			233–265		3C
<i>Limea</i> (2)		123–240	123–240		2D
<i>Limea</i>			374–442	IB.mc	2D/3B
<i>Notolimea</i>		122–127	122–127		2D
<i>Notolimea</i> (2)	150	206–390	206–390		2D

#### EGG SIZE, ENERGY CONTENT, AND NUTRITION

Egg size (yolk mass diameter, volume) is probably the most important parameter for inferences on early life history traits of

marine invertebrate larvae; in bivalves, its application dates back to THORSON (1946, 1950) and OCKELMANN (1959, 1965), primarily as a means to distinguish between planktotrophic and lecithotrophic development. However, as also discussed in the

TABLE 7. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorpha: Malleidina (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Pinnoidea					
<i>Atrina</i> (3)	35–65	67–85	370–620	Op	2A
<i>Pinna</i> (3)	80	64	296–400	Op	2A
Pterioidea					
<i>Malleus</i>		<100	265–325		2A
<i>Pinctada</i> (4–5)	47–89	67–85	210–366	Op	2A
<i>Pteria</i> (2)	33–37	81		Op	2A
<i>Pulvinites</i>		289–299	550–616	IB.ct (dv)	2B
<i>Bakevelliid</i> spp. (7) (F)		60–102	297–745		2A



TABLE 8. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorphia: Ostreidina (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
<i>Exogyra</i> (2) (F)		50–<100	273–304		2A
<i>Pycnodonte</i> (2) (F)		65–83	303–356		2A
<i>Parahyotissa</i>		70–85	308–372		2A
<i>Liostrea</i> (F)		67–100	360–520		2A
<i>Agerostrea</i> (F)		62–88	331		2A
<i>Cubitostrea</i> (3) (F)		49–79	245–456		2A
<i>Odontogryphaea</i> (F)		<100	–400		2A
<i>Crassostrea</i> (F)		61–82	346–421		2A
<i>Saccostrea</i> (F)		59–79	326–378		2A
<i>Crassostrea</i> (4)	45–62	50–78	248–400	Op	2A
<i>Sacc/Striostrea</i> (5)	36–49	50–76	226–350	Op	2A
<i>Ostrea</i> (4)	60–110	105–140	284–377	IB, IB.ct (dv)	2A
<i>Ostrea</i> (4)	100–150	162–200	240–360	IB.mc (dv), IB	2B
<i>Ostrea</i> (2)	200–312		390–521	IB.mc	3A
<i>Ostrea</i> (F)			443–470		3A

section on Developmental Modes (p. 59, herein), nourishment is often mixotrophic or facultatively planktotrophic (MCEdWARD, 1997; ALLEN & PERNET, 2007), suggesting a continuous rather than a bimodal distribution of egg dimensions, which should discourage the definition of size boundaries. Other autecologic and environmental factors that probably influence egg size include brooding time, matrotrophy, and temperature, among others (see MORAN & McALISTER, 2009, for other variables). More importantly, however, the efficacy of the most common method of inference depends on the assumed proportionality between egg diameter and energy content, which has been questioned in recent years (MORAN & McALISTER, 2009; see also McALISTER & MORAN, 2012, on echinioids).

Unfortunately, egg energy content is unknown for most invertebrates, including bivalves, so that assumptions on its correlation with egg size are rather speculative. The bivalve prodissoconch-1 adds yet another

parameter for inferences, which is not available in most other groups (except, for example, other Mollusca, Brachiopoda). Conflicting evidence on the utility of prodissoconch-1 dimensions as predictors of egg size has prompted us to explore this issue further.

#### YOLK MASS AND P-1 PARADOXES

ALLEN and SANDERS (1973) observed that strictly lecithotrophic siliculid and lametilid protobranchs have small eggs (70–90  $\mu\text{m}$  in diameter), similar to those of autobranch bivalves with obligatory planktotrophic development. In addition, they recorded P-1 sizes between 200  $\mu\text{m}$  and 580  $\mu\text{m}$  in these protobranchs, which seem unrelated to egg size and much larger than would be predicted based on OCKELMANN'S data for autobranchs (Tables 1, 15; cf. OCKELMANN, 1965, fig. 1). ALLEN and SANDERS (1973, p. 307) concluded, therefore, that “in the light of the data presented by OCKELMANN (1965) for lamellibranchs [autobranchs],

TABLE 9. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pteriomorpha: Carditida (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; measurements in brackets are considered dubious; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Astartidae					
<i>Nicaniella</i> (3) (F)		90–152	152–212		2B
<i>Oxyeurax</i> (F)		143	211		2B
<i>Pressastarte</i> (2) (F)		140–157	140–157		2D
<i>Astarte</i> (5)	110–200			?O:jc	
<i>Astarte</i>	312	254–264		jc	
<i>Goodallia</i> (4)		158–179	179–210		2C
<i>Goodallia</i>		275	329		2C
Crassatellidae					
<i>Crassinella</i> (F)		62–88	130–161		2B
<i>Crassinella</i> (F)		160–170	184–187		2C
<i>Pteromeris</i>		178	210		2C
<i>Salaputium</i>		193–201	193–201		2D
Carditidae					
<i>Cardita</i>		120	260		2A
<i>Cardita</i>		240–257	275–298		2C
<i>Carditella</i>		130–157	130–157		2D
<i>Carditella</i>			360	IB (j)	3C
<i>Cardites</i>		164–168	177–182		2C
<i>Cyclocardia</i> (3)	[500–580]	[591]	[550–750]	IB, IB.ctp (av-j)	2C?
<i>Cyclocardia</i>	339	264–286		jc	
<i>Glans</i>		172–174	190–193		2C
Condylocardidae					
<i>Austrocardiella</i> (3)			420–460	IB, ?	3C, 3B/3C
<i>Benthocardiella</i> (2)			370–500		3C
<i>Carditopsis</i> (2)		130–225	130–225	?, IB	2D, 2D/3C
<i>Condylocardia</i> (10)			286–480	IB, IB (j), IB.sct, ?	3C, 3B/3C
<i>Isodontocardia</i>			180		2C/3C
<i>Condylocuna</i> (4)			320–520	IB, IB (j), ?	3C, 3B/3C
<i>Crassacuna</i> (3)		110–210	110–210		2D
<i>Cuna</i> (9)		160–300	160–300		2D, ?2C/2D
<i>Cuna</i> (2)		160–180	170–190		2C
<i>Cunanax</i> (4)			820–1380		3B, 3B/C, 3C
<i>Mimicuna</i>			240–290	IB (j?)	3C
<i>Ovacuna</i>	113–126		130–200		2D/3B
<i>Propecuna</i>		180–230	180–230		2D
<i>Warrana</i> (4)		140–210	170–220		2C
<i>Warrana</i> (10)			140–330		2D, 2D/3C, ?2C
<i>Westaustrocuna</i> (2)		150–162	170–182		2C

it would seem to be a paradox in that egg size [of protobranchs] would indicate planktotrophic/lecithotrophic development whereas prodissoconch size would indicate lecithotrophic/direct development.”

In order to explore this paradox, we compared the relationships between egg size (ymd) and P-1 length, as well as the ranges of the egg-size/P-1 ratio in protobranchs and autobranchs. Where appropriate, we

TABLE 10. Distribution of egg size, shell characters, and mode of development in autobranch genera of Euheterodonta, orders Lucinida and Cardiida (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Lucinida					
<i>Codakia</i>	92–110	120–170	170–200	O.jc (dv)	2C
<i>Lucinoma</i>	200	?	<240	O.jc	?2C
<i>Parvilucina</i>		140	166–198		2C
<i>Phacoides</i>		190–206	190–206	EB.bs.jc (av)	2D
<i>Adontorhina</i> (2)		130–145	130–145		2D
<i>Axinulus</i> (2)		131–147	131–147		2D
<i>Axinopsida</i>	160–175	300	300		2D
<i>Mendicula</i>		159–171	159–171		2D
<i>Sinbadiella</i> (F)		90–97	195–207		2A
<i>Thyasira</i> (6)	>120	148–182	148–182		2D
<i>Thyasira</i> (1)	160–190	205–270	205–270	Ob.jc	2D
Cardiida					
Cardioidei					
Cardioidea					
<i>Parvicardium</i>	64	90	~250	O.jc (dv)*	2A
<i>Ceastoderma</i>	50	<140	300	Op.jc (dv)	2A
Tellinoidea					
<i>Donax</i> (2)	75	70–95	250–350	Op	2A
<i>Gari</i>		104	272		2A
<i>Rocheffortina</i>		75–85	240–248		2A
<i>Scrobicularia</i>	75–80	106	250–270	O.jc (dv)	2A
<i>Macoma</i> (2)	60–114	155	350	O	2A
<i>Macoma</i> (2)	160–260		315–460		?

excluded ST-3 dimensions from the analyses because the size of the P-1 stage cannot be determined with certainty in taxa exhibiting that shell type. Also, visual inspection of the size data for Protobranchia (Table 15) seemed to indicate that the three siliculid and one lametilid species that gave rise to the paradox could be outliers. Therefore, we analyzed the data including and excluding those four values.

With all observations included, protobranch egg and P-1 sizes appear to be poorly correlated, which strongly contrasts with the relationship between these variables in Autobranchia (Fig. 39.1–39.2). In light of the fact that the protobranch P-1 grows within the pericalymma, this result would primarily

suggest that egg dimensions are poor predictors of the size of the metamorphosing pericalymma. However, if siliculid and lametilids are excluded, the results suggest a strong correlation of the two variables (Fig. 39.3). Both interpretations would be consistent with data provided by GUSTAFSON and REID (1986), GUSTAFSON and LUTZ (1992), and ZARDUS and MORSE (1998) (Table 16), but too few observations on pericalymma size are available for statistical treatment. For Autobranchia, the exclusion of species with ST-3 does not significantly alter the outcome (Fig. 39.4).

The comparison of egg/P-1 ranges including siliculids and lametilid suggests that means differ significantly between

TABLE 11. Distribution of egg size, shell characters, and mode of development in autobranch genera of Veneroidei (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Veneroidei					
Arcticoidea					
<i>Arctica</i>	68–95				
<i>Coralliophaga</i>		72–97	138–166		2B
Cyamoidea					
<i>Gaimardia</i> (2)	220–260			IB.ct	3B, ?
Cyrenoidea					
<i>Corbicula</i> (2)	140–170			IB.ctp	
Galeommatoida					
<i>Divariscintilla</i> (5)		120–155	332–428	IB.sct, IB.ct-sct (dv), ?	2A
<i>Kellia</i>	25–50	64–80	300–370	IB (dv)	2A
<i>Hyalokellia</i>		135	300–325		2A
<i>Borniola</i>		150–190	325–375		2A
<i>Lasaea</i> (2)		75–115	220–300	IB (dv)	2A
<i>Lasaea</i> (2)		100–170	300–680	IB.ct (av or j)	3A
<i>Lasaea</i>	300		600	IB.ct (j)	3A?
<i>Altenaeum</i>			~715		3A
<i>Kurtiella</i> (4)	75	100–150	307–500	IB (dv)	2A
<i>Kurtiella</i>			440–530		3A
<i>Montacuta</i> (2)	57–63	120–150	275–385	IB.sct	2A
<i>Mysella</i>	217		379–550	IB.ct, IB.sct	3A
<i>Mysella</i> (2)		126–186	265–370	IB.ctp	2A
<i>Rochefortula</i>		~130	~350		2A
<i>Tellimya</i> (4)	45–90	90–137	300–420	IB.sct (dv, ?j)	2A
<i>Thecodontia</i>		130	420–450		2A
Glossoidea					
<i>Kelliella</i>		75–120	158–199		2B
<i>Vesicomya</i> (2)		165–200	165–200		2D
<i>Waisiuconcha</i>		160	160		2D
Veneroidea					
<i>Lutetina</i>			250		3B
<i>Neolepton</i> (3)		136–175	195–240	?IB	2B, 2C
<i>Turtonia</i>	145–170		260–315	EB.bs.jc	3A
<i>Anomalocardia</i>	60	<95	300–340		2A
<i>Chamelea</i>	54	110	260	Op	2A
<i>Chione</i> (1–2)	60–74	87–<125	170–252		2B
<i>Clausinella</i>	60	110	276		2A
<i>Hyphantosoma</i>		125–130	250–300		2A
<i>Lirophora</i>		83–113	198–234		2A
<i>Meretrix</i>	60–75			Op	?
<i>Timoclea</i>		80–90	160–180		2B
<i>Venerupis</i> (2)	60–63	90–100	260–300		2A
<i>Venus</i>	69	100	280		2A

TABLE 12. Distribution of egg size, shell characters, and mode of development in autobranch genera of Pholadata (Pholadida) and Anomalodesmata (Septibranchida; Pholadomyida: Pandoroidei, Thracioidei) (see text for details). Taxa are ordered alphabetically within families or subfamilies. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; measurements in brackets are considered dubious; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Pholadata					
Pholadoidea					
<i>Barnea</i> (2)	40–45	55–95	250–370		2A
<i>Zirphaea</i>	40	76–92	340–360	IB (dv)	2A
<i>Xylophaga</i> (2)	70		280–310	IB	2A
<i>Xylophaginae</i> sp.		55–60	304	E.dw	2A
<i>Xylophaga</i> (5)			300–400	E.dw?	2A
<i>Xylophaga</i> (2)			600–1000	IB.dw?	
<i>Teredo</i>	50–60	65–90	190–250	IB (av)	2A
<i>Zachsia</i>		80	208	IB.dw (dv)	2A
Septibranchida					
Cuspidarioidea					
<i>Cardiomya</i>			172, 200		2D, ?
<i>Cuspidaria</i> (3)	115–165	153–190	153–190	jc	2D
<i>Cuspidaria</i>	185–200				
<i>Halonymphea</i>		161–184	161–184		2D
<i>Rengea</i>	125–135	155	155		2D
<i>Rhinoclama</i>	180				
Poromyoidea					
<i>Cetomya</i>	140				
<i>Poromya</i>	175			jc	
Verticordoidea					
<i>Lyonsiella</i>	150			jc?	
<i>Policordia</i>	120–150				
<i>Euicroa</i> (2)	300		330–350		
Pandoroidei					
<i>Laternula</i> (1–2)	120–220	183–216	214–265	O.jc	2C
<i>Lyonsia</i> (2)	100–190		155–175	O.jc	
<i>Pandora</i> (2)	105–145	[150]	155–200	O.jc, O.jc (tr)	2C
Thracioidei					
<i>Thracia</i>	55	107	245	?O.jc	2A
<i>Thracia</i> (3)	100	150–158	180–190		2C
<i>Thracia</i>	160–170	247	339	IB.jc	2B

the two subclasses under the assumption of equal variance ( $p = 0.033$ ), but they do not differ if unequal variance is allowed, which seems more realistic ( $p = 0.062$ ) (Fig. 40.1). The hypothesis of true difference between the means is rejected, with or without the assumption of equal variance, when these problematic taxa are excluded ( $p = 0.812$  and  $0.815$ , respectively) (Fig. 40.2).

These results do not clearly indicate whether siliculid and lametilid protobranch measurements are outliers or whether the reported shell dimensions reflect nepioconch rather than prodissococonch sizes. Restudying the shells should shed light on this issue. In any case, it seems clear that more data on protobranchs are needed to clarify the relationships between egg, pericalymma, and P-1 dimensions. Establishing these

TABLE 13. Distribution of egg size, shell characters, and mode of development in autobranch genera of Solenata (see text for details). Taxa are ordered alphabetically within families or sub-families. Multiple appearance of genera refers to intrageneric grouping according to similarities in egg size, shell size, or shell type. Measurements are in  $\mu\text{m}$ ; egg size is yolk mass diameter (assumed). Parenthetical numbers following generic names indicate number of species (ranges of numbers in parentheses indicate suspected number of species). Overall shell length is either P-1, P-2, or metaconch/cryptoconch, depending on shell type. Question marks (?) indicate that the developmental mode or shell type is unknown for one or more species. See caption of Table 3 for explanation of abbreviations (new).

Taxon	Egg size	P-1 length	Overall shell length	Developmental mode	Shell Type
Solenida					
<i>Ensis</i> (2)	64–75	80–109	210–416	Op, Op.?jc	2A
<i>Siliqua</i>	>90	105–115	300	Op	2A
<i>Solen</i>	110–141	166–175	285–320	?O,jc	2B
Hiatellida					
<i>Hiatella</i> (2)	70–80	70–103	303–362	Op	2A
<i>Hiatella</i> (F)		80	250		2A

relationships would allow indirect evaluation of possible differences in nutritional requirements and egg energy contents.

#### P-1/P-2 RATIO

The P-1/P-2 ratio is here deemed to be a rough estimator for the lecithotrophy/planktotrophy ratio, or more generally, the relative endotrophy/exotrophy dependence of a developing autobranch larva. Theoretically, therefore, one should find a stepwise increase in yolk mass diameter and P-1 size from ST-2A to ST-2D. As before, ST-3 is not included in this argument because its

indistinct stage boundaries hamper measurements.

Yolk mass diameters of the four subtypes of ST-2 fall into two size-range groups, small ( $\leq 90 \mu\text{m}$ ) and medium/large (essentially  $\geq 100 \mu\text{m}$ ), which correspond to ST-2A and ST-2B-2C-2D, respectively (Fig. 41.1). That there are two, rather than four, groups is not surprising, however, considering that ST-2A represents P-1/P-2 ratios from 0 to 0.5, and all other shell types together have ratios from 0.5 to 1. This only suggests that the second group was overly subdivided, as far as yolk mass diameter is concerned.

TABLE 14. Taxonomic composition of the dataset on early ontogenetic shells and developmental modes used herein (new).

Higher taxa	Families	Species (fossil)	Species (all)
Bivalvia	74	47	620
Euprotobranchia	1	1	1
Fordillida	1	1	1
Protobranchia	10	1	57
Nuculida	1	0	25
Solemyida	1	0	4
Nuculanida	8	1	28
Autobranchia	63	45	562
Pteriormorphia	20	31	239
Trigoniida	1	1	2
Unionida	2	0	83
Carditida	4	11	92
Euheterodonta	36	2	146

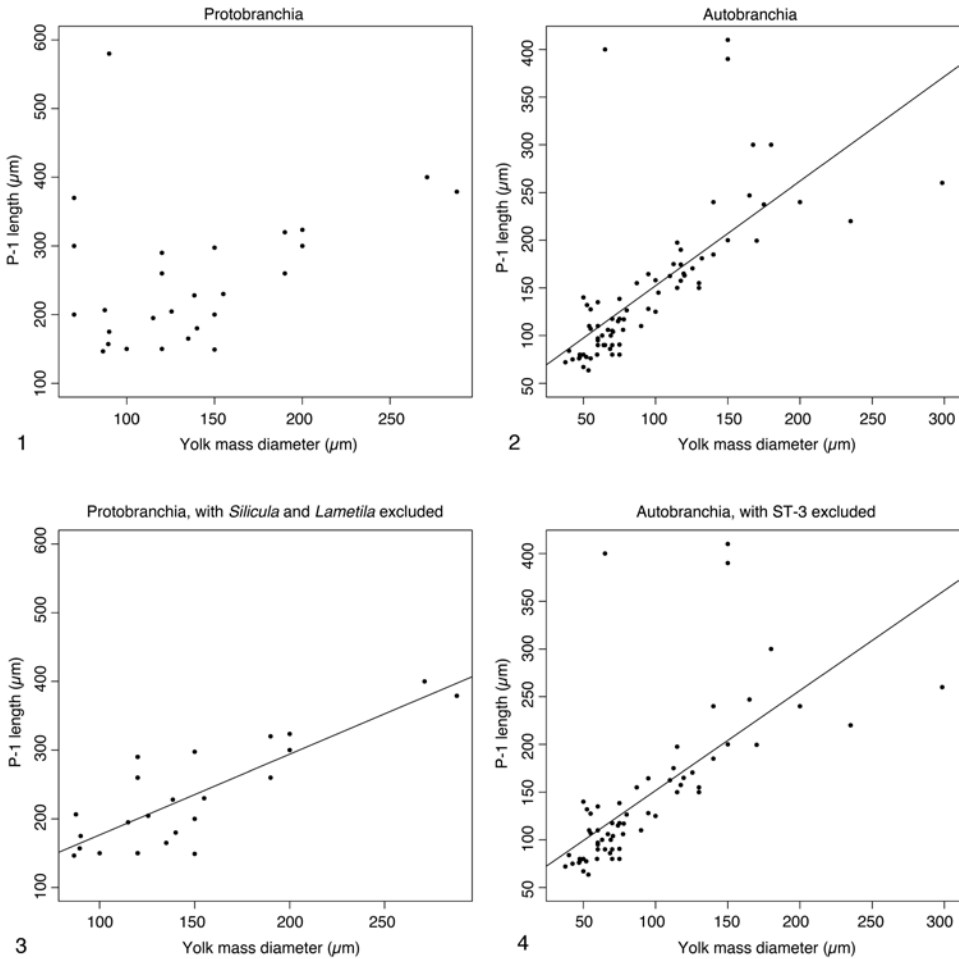


FIG. 39. Relationship between prodissoconch-1 length and yolk mass diameter in protobranch (1, 3) and autobranch (2, 4) bivalves; 1, hypothesis of noncorrelation between variables could not be rejected (Pearson's  $r = 0.324$ ,  $t(25) = 1.714$ ,  $p = 0.099$ ,  $N = 27$ ); 2, straight line shows best fit of linear regression ( $R^2 = 0.50$ ,  $p < 0.001$ ,  $N = 76$ ); 3, with the genera *Silicula* JEFFREYS, 1879, and *Lametila* ALLEN & SANDERS, 1973 excluded from analysis, hypothesis of noncorrelation is rejected (Pearson's  $r = 0.836$ ,  $t(21) = 6.983$ ,  $p < 0.001$ ,  $N = 23$ ); straight line shows best fit of linear regression ( $R^2 = 0.70$ ,  $p < 0.001$ ,  $N = 23$ ); 4, excluding taxa with ST-3 from analysis has little effect (linear regression:  $R^2 = 0.46$ ,  $p < 0.001$ ,  $N = 65$ ) (new).

Comparing the medians, the difference between the two groupings reflects a doubling of yolk mass diameter (~60 µm and 120 µm, respectively), which is equivalent to a 6- to 8-fold increase in yolk volume. In this respect, the group of small eggs may be called yolk poor, and the second group of medium/large eggs, yolk rich. As will be seen later, there are two more groups of large

and very large eggs (>200 µm and >300 µm, respectively), comprising mainly taxa exhibiting ST-3; however, these egg sizes are rare. Indeed, small eggs (≤90 µm) tend to indicate a strong dependence on exotrophy (mainly planktotrophy), but the upper boundary is fuzzy due to brooding and probably other factors (see discussion of Autobranchia below, p. 76, herein).

TABLE 15. Egg sizes, shell characters, and mode of development in the euprotobranch *Pojetaia runnegari* JELL, 1980, and eubivalvian protobranch genera (see text for details). Egg sizes are assumed yolk mass diameters. Multiple appearances of genera refer to intrageneric grouping according to similarities in egg size, shell size, or shell type. Parenthetical numbers following generic names indicate number of species ( $n > 1$ ); asterisk (\*) marks instances in which developmental mode is inferred from source; *I(A)*, *I(B)*, assumed according to source text; question marks (?) indicate that the mode is unknown for one or more species. Subsequent cells (of a row) summarize present knowledge. Blank cells are gaps in knowledge. *F*, fossil genus; *EB.bs*, external brooding in a brood sac; *I*, internal brooding; *IB(j)*, internal brooding and release as juvenile; *j*, juvenile; *O*, oviparous; *Ob*, oviparous-benthic; *Op*, oviparous-pelagic; *I*, protobranch shell type (unspecified); *IA*, Shell Type 1A; *IB*, Shell Type 1B; *IC*, Shell Type 1C; *IA/B*, Shell Type 1A or 1B but not 1C; *IB/C*, Shell Type 1B or 1C but not 1A (new).

Taxon	Yolk mass diameter	P-1 length	Developmental mode	Shell Type
Fordillida				
<i>Pojetaia</i> (F)		175		1(A)
Nuculida				
<i>Acila</i> (2)	120–160	150–230	Op, ?	1(A)
<i>Austronucula</i>		176–200		1B
<i>Brevinucula</i>	134–143	226–230		1(A)
<i>Condylonucula</i> (3)		160–220		1C
<i>Deminucula</i>	117–134	198–211		1B
<i>Ennucula</i>	98–102	146–154		1B
? <i>Ennucula</i>	130–140			1
<i>Ennucula</i> (3)	200–294	300–385		1B, 1(B)
<i>Nucula</i> (4–7)	83–150	131–200	Op, ?	1B, 1(A)
<i>Nucula</i> (2)		240–380	IB (j*), ?	1C, 1B/C
<i>Nucula</i> (3)	190–210	270–332	EB.bs, IB, ?	1B
<i>Pristigloma</i>	115	190–200		1A/B
<i>Pristigloma</i>	190	260		1A/B
<i>Solemyoidea</i>				
<i>Acharax</i>		1350		1A/B
<i>Solemya</i> (3)	190–271	280–440	Ob, Op, ?	1A/B
Nuculanoida				
<i>Mesosacella</i> sp. (F)		157		1A
<i>Tindariopsis</i>		275–283		1(B)
<i>Lametila</i>	70	370		1
<i>Praelametila</i>		190		1
<i>Nuculana</i> (4)	120–150	135–204		1B, 1(A)
<i>Nuculana</i>	>150	245–350		1
<i>Nuculana</i>		580–660		1
<i>Silicula</i> (2)	70	200–310		1
<i>Silicula</i>	90	580		1
<i>Microgloma</i>	85–90	195–218	IB (j)	1B
<i>Microgloma</i> (3)	120	260–290		1A/B, 1(A)
<i>Portlandia</i>	140			1
<i>Yoldia</i> (2)	145–150	200	O, ?	1
<i>Yoldiella</i> (3)	105–120	190–215		1A, 1

Prodissoconch-1 lengths reveal three groups with significantly distinct mean values (Fig. 41.2): ST-2A, ST-2B, and ST-2C-2D. These groups cover the lower 50%, middle 25%, and upper 25% of the range of P-1/P-2 ratios. Overall, P-1 length increases from ST-2A to ST-2D, indicating decreasing

P-2 lengths and thus decreasing exotrophic dependence until ST-2D is reached. Why this increase is not correlated with an increase in yolk mass diameter, as could be expected from Figure 39.2, is presently unclear and requires further analysis. From a practical point of view, yolk mass diameter allows one



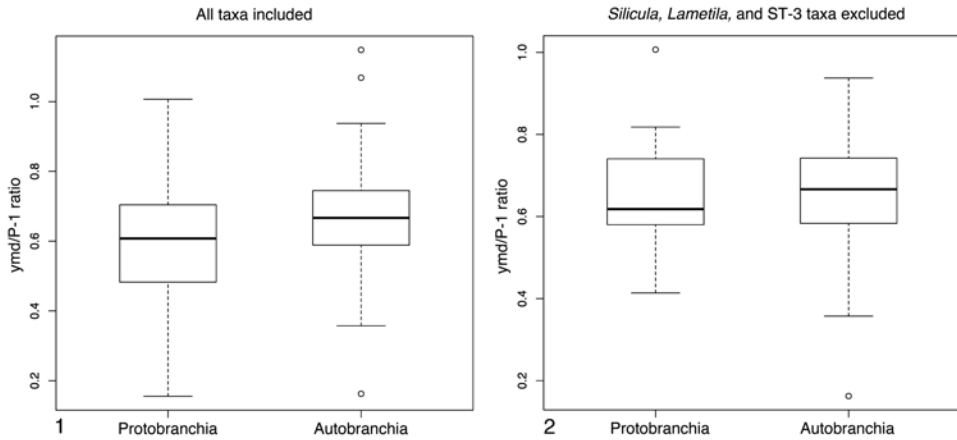


FIG. 40. Boxplots of the yolk mass diameter/P-1 length (ymd/P-1) ratio for protobranch and autobranch bivalves; 1, with all taxa included, the hypothesis of difference between the true means of the two groups cannot be rejected under the assumption of equal variance, but support for a significant difference is weak (see text for details); two Sample  $t$ -test:  $t(101) = -2.166, p = 0.033$ ; Welch Two Sample  $t$ -test:  $t(37.684) = -1.919, p = 0.062$ ; 2, with *Silicula* JEFFREYS, 1879, *Lametila* ALLEN & SANDERS, 1973, and taxa displaying ST-3 excluded from analysis, hypothesis of difference between true means is rejected (Two Sample  $t$ -test:  $t(95) = -0.238, p = 0.812$ ) (new).

to distinguish yolk-poor from yolk-rich eggs, which correlates with high versus decreasing dependence on additional energy supply for the second larval growth phase; P-1-length allows a more detailed subdivision of shell types but not of nutritional needs; and the P-1/P-2 ratio is needed to distinguish all four subtypes. Note that the distinction between yolk-poor and yolk-rich eggs resembles the split between planktotrophic and nonplanktotrophic proposed by JABLONSKI and LUTZ (1983). However, these categories are insufficient to infer specific development modes and may be misleading in certain contexts.

### TAXONOMIC PATTERNS IN DEVELOPMENT PROTOBRANCHIA

Table 15 provides an overview of early-life history characters for protobranchs, indicating that egg sizes in the group range from 70  $\mu\text{m}$  to 300  $\mu\text{m}$  ( $n = 34$ ). However, most eggs (90%) do not surpass 200  $\mu\text{m}$  (Fig. 42). A taxonomic bias is not evident. As there is no other evident energy source, all protobranch eggs are assumed to allow fully lecithotrophic development of the pericalymma larva.

TABLE 16. Comparison of developmental types and larval dimensions of three protobranch species. All measurements in  $\mu\text{m}$ ; 1, ZARDUS and MORSE (1998); 2, GUSTAFSON and REID (1986); 3, GUSTAFSON and LUTZ (1992); asterisk (\*), size at metamorphosis (juvenile hatch size is 400  $\mu\text{m}$ ) (new).

Species	Development type	Egg size	Pericalymma size	Prodissoconch size
<i>Acila castrensis</i> (1)	planktonic, free swimming	120	170	150
<i>Solemya reidi</i> (2)	benthic encapsulated, then free swimming	271 (capsule 465–566)	360–440	433 $\pm$ 42
<i>Solemya velum</i> (3)	benthic, in egg capsule, hatching juvenile	190	400	320*

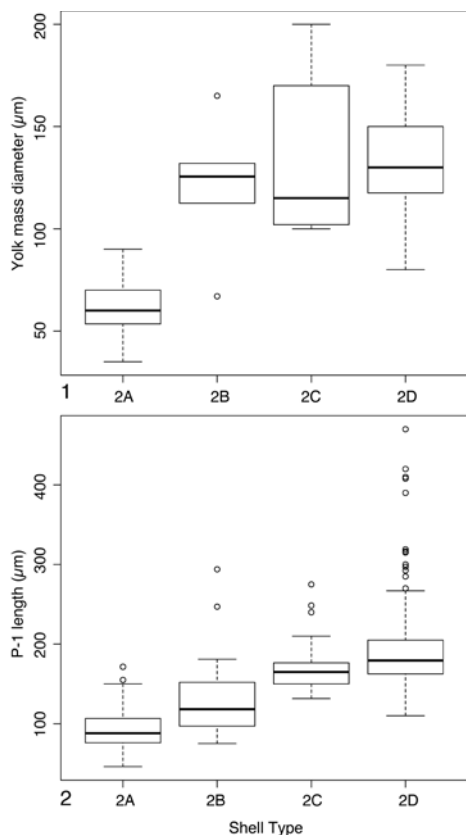


FIG. 41. Boxplots of yolk mass diameter (1) and P-1 length (2) for Shell Types 2A to 2D; results of Tukey multiple comparisons of means ( $H_0$ : true difference in mean among shell types equals zero). 1, 2A–2B,  $p < 0.001$ ; 2A–2C,  $p < 0.001$ ; 2A–2D,  $p < 0.001$ ; 2B–2C,  $p = 0.639$ ; 2B–2D,  $p = 0.611$ ; 2C–2D,  $p = 0.993$ ; 2, 2A–2B,  $p = 0.001$ ; 2A–2C,  $p < 0.001$ ; 2A–2D,  $p < 0.001$ ; 2B–2C,  $p = 0.024$ ; 2B–2D,  $p < 0.001$ ; 2C–2D,  $p = 0.060$  (new).

Developmental modes are benthic (demersal), benthic-planktonic, planktonic, or brooded (Table 15). The nuculid *Acila castrensis* (HINDS, 1843) is a broadcast spawner with sticky, negatively buoyant eggs and a planktonic development of a swimming larva. The shell is uncalcified at metamorphosis (ZARDUS & MORSE, 1998). Larvae of *Solemya reidi* BERNARD, 1980, hatch from a benthic egg capsule and are active, negative geotactic swimmers, suggesting a planktonic life (GUSTAFSON & REID, 1986). In contrast,

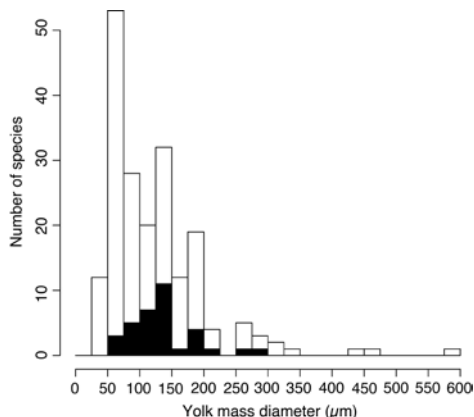


FIG. 42. Frequency histogram showing the distribution of egg sizes in bivalves. White and black bars correspond to autobranchs and protobranchs, respectively (new).

*Solemya velum* SAY, 1822, metamorphoses within its benthic egg capsule and hatches as a juvenile (GUSTAFSON & LUTZ, 1992); the shell of the hatching bivalve is a metaconch with a well-marked prodissoconch-1/nepioconch boundary. *Nucula delphinodonta* MIGHELS & ADAMS, 1842, develops within an external brood sac attached to the female shell (DREW, 1899), whereas several other *Nucula* species and *Microgloma pusilla* (JEFFREYS, 1879) are internal brooders, probably to the early juvenile stage (OCKELMANN & WARÉN, 1998; KILBURN, 1999).

The largest P-1 sizes are found in the orders Nuculanida ( $\leq 660 \mu\text{m}$ ) and Solemyida ( $\leq 440$ , exceptionally  $1350 \mu\text{m}$ ); most other larval shells range from  $130 \mu\text{m}$  to  $380 \mu\text{m}$  (Table 15). As discussed above, probable correlation between prodissoconch-1 size and yolk mass diameter requires confirmation (Fig. 39.1, Fig. 39.3).

Correlation patterns between Shell Types 1A–C and developmental mode are not evident, which may be a result of insufficient knowledge. Special brooding conditions are at least suspected for *Condylonucula* and some *Nucula* spp. based on the similarity between their ST-1C and the autobranch ST-3C (see below).

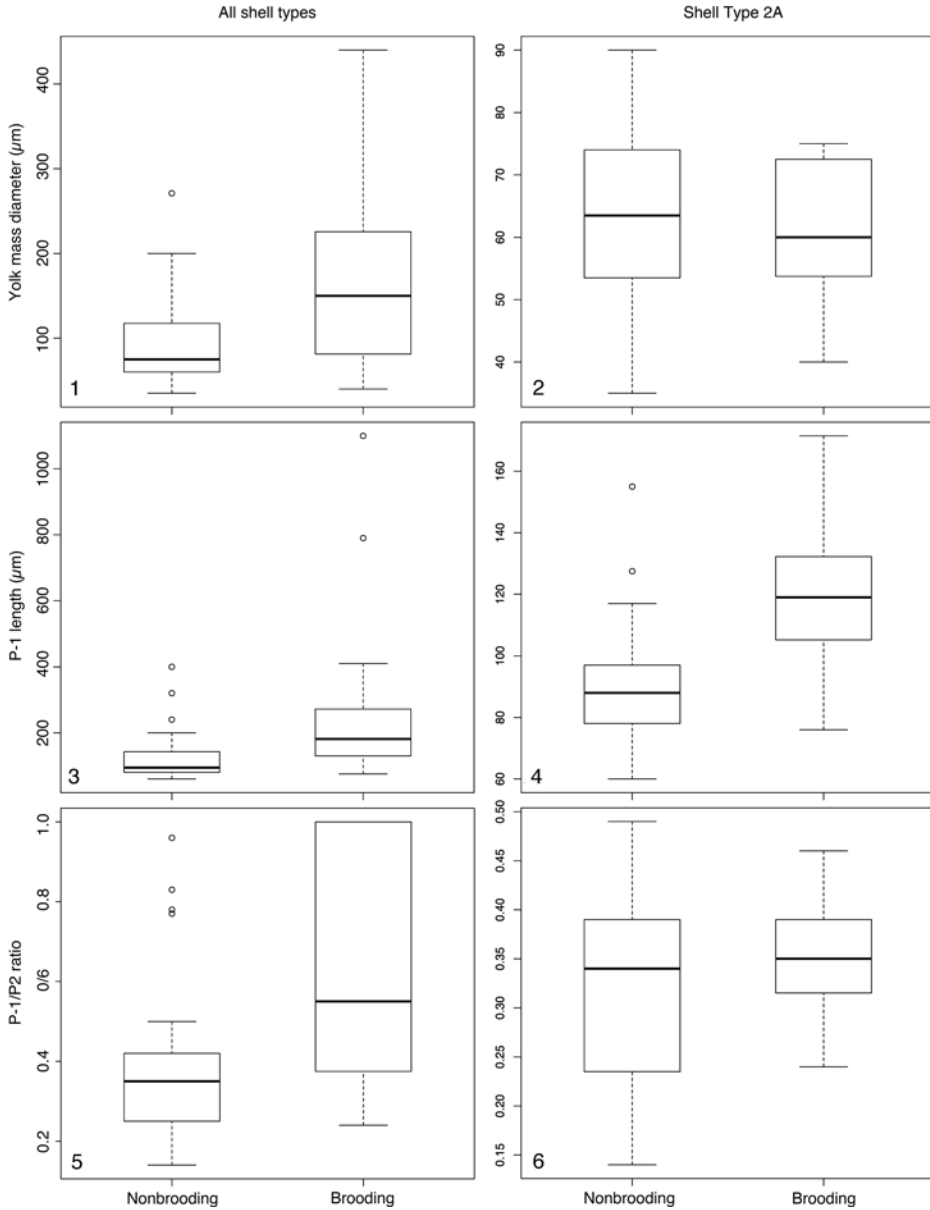


FIG. 43. Boxplots showing ranges of yolk mass diameter, prodissoconch-1 (P-1) length and prodissoconch-1/prodissoconch-2 (P-1/P-2) ratio for nonbrooding (n-br) and brooding (br) species in all observed species (1, 3, 5) and in species displaying Shell Type 2A (2, 4, 6). Two sample  $t$ -test results ( $H_0$ , true difference in mean between nonbrooding and brooding groups equals zero): 1,  $t(76) = -4.198$ ,  $p < 0.001$ ; 2,  $t(31) = 0.469$ ,  $p = 0.642$ ; 3,  $t(95) = -4.201$ ,  $p < 0.001$ ; 4,  $t(50) = -4.411$ ,  $p < 0.001$ ; 5,  $t(75) = -5.054$ ,  $p < 0.001$ ; 6,  $t(49) = -1.472$ ,  $p = 0.147$ . Number of observations: 1, n-br = 51, br = 27; 2, n-br = 26, br = 7; 3, n-br = 52, br = 45; 4, n-br = 37, br = 15; 5, n-br = 41, br = 36; 6, n-br = 36, br = 15 (new).

## AUTOBRANCHIA

Fully grown, competent eggs range from ~25 to 580  $\mu\text{m}$  ( $n = 143$ ). As in Protobranchia, autobranches show a marked positive skew in the distribution of egg sizes (egg sizes below 200  $\mu\text{m}$  represent 91% of observations), but differ by extending the size range below 70  $\mu\text{m}$  and above 300  $\mu\text{m}$ . Egg size (y<sub>md</sub>) and P-1 length are highly correlated (Fig. 39.2, Fig. 39.4), which corroborates results from OCKELMANN (1965) and MORAN (2004b, fig. 2).

Table 2 provides a condensed overview of early-life-history characters. Brooding occurs with all shell types, but the presently available data suggests a gap between ratios 0.6 to 0.9 (part of ST-2B and ST-2C; Fig. 36), in which only one instance of brooding was observed. The reasons for this gap are unclear, and we cannot presently exclude sampling bias. Numerous instances of brooding were recorded in taxa with ST-2A (Fig. 36); otherwise, this shell type is identical to OCKELMANN'S (1965) category of planktotrophic larvae (compare with Table 1). All nonbrooding subgroups from ST-2A to ST-2D contain a few species that shed eggs with a protective gelatinous coat (jelly coat, egg capsule of authors; COLLIN & GIRIBET, 2010). In at least some species, these eggs release D-veligers, as do most brooders. Only species of *Teredo* LINNAEUS, 1758, and *Lyrodus* GOULD, 1870 (Teredinidae), are hitherto known to release advanced veligers with well-developed P-2 (SHIPWAY, 2012).

On a coarse scale, the number of brood variants and developmental stages at release increases from ST-2A to ST-2D (Table 2). Species with type-3 shells produce fewer variants, but all are internal brooders, except *Turtonia minuta* (FABRICIUS, 1780) (EB.bs in Table 2). Offspring is either released as an advanced veliger (typically ST-3A), or as a juvenile displaying a metaconch or cryptoconch (ST-3B to 3C).

Despite considerable overlap, nonbrooding and brooding species are significantly different in mean yolk mass diameters, P-1 size, and

P-1/P-2 ratios (Fig. 43). The nonbrooding group includes species with jelly-coated eggs, some of which extend the upper range of egg sizes to 200  $\mu\text{m}$  [e.g., *Laternula elliptica* (KING & BRODERIP, 1832), *Lucinoma aequizonata* (STEARNS, 1890)], whereas other species have egg sizes slightly below the median of 75  $\mu\text{m}$  [*Ensis* SCHUMACHER, 1817; *Parvicardium exiguum* (GMELIN, 1791 in 1791–1793)].

The same analysis restricted to species with Shell Type 2A identifies only P-1 mean sizes as statistically different in nonbrooding and brooding species (Fig. 43.2, Fig. 43.4, Fig. 43.6). Overall, P-1 size is the most reliable, though not infallible, indirect parameter to distinguish between brooding and nonbrooding taxa.

## TAXONOMIC PATTERNS IN RECENT AUTOBRANCHIA

### Mytilida

Mytilids produce eggs measuring ~45  $\mu\text{m}$  to 440  $\mu\text{m}$ , and their larval shells are essentially restricted to types 2A and 2D (Table 3). All Bathymodiolinae seem to be characterized by ST-2A (OLU-LE ROY & others, 2007, and references therein). The crenelline *Rhomboidella obesa* OCKELMANN, 1983, possesses a 2D shell, although its egg measures only 80  $\mu\text{m}$  in diameter; its developmental mode is unknown. All other mytilids with ST-2D, and whose developmental mode is known, brood their larvae either internally, in the mantle cavity or posterodorsal brood chamber, as in *Dacrydium viviparum* OCKELMANN, 1983, and *D. albidum* PELSENEER, 1903 (OCKELMANN, 1983; HAIN & ARNAUD, 1992), or externally, in an egg string or byssus nest (e.g., *Musculus* RÖDING, 1798; THORSON, 1935; MERRILL & TURNER, 1963; OCKELMANN, 1983). According to DINESEN (personal communication, 2005), *Crenella decussata* (MONTAGU, 1808) "lays egg masses in the exhalant tube of its own nest (in fine gravel/shell sand). Once the development is completed, the young crawl to the sediment surface and take up separate life, first as nepioconchs and later as dissoconchs."

Shells smaller than 210  $\mu\text{m}$  are symmetrical ST-2D, whereas larger shells (210–540  $\mu\text{m}$ ) tend toward ST-3B: *D. balgimi* SALAS & GOFAS, 1997; *D. viviparum* OCKELMANN, 1983; or ST-2D/3A in *Musculus svecicus* (FABRICIUS, 1788) [shape inferred from drawings in THORSON, 1935, cited as *Modiolaria nigra* (J. E. GRAY, 1824)]. In *Dacrydium* TORELL, 1859, small ST-2D shells could be related to external development (either protected or unprotected) and the larger 2D/3B type to internal brooding. However, this observation requires confirmation and does not hold for other higher taxa.

### Arcida

The early ontogenetic shell typology of arcoids is much more diverse, with all ST-2 and ST-3 subtypes represented but ST-3A (Table 4). Some subtypes are rather typical of particular genera. For example, most species of *Limopsis* SASSI, 1827, develop the typical equilateral ST-2D, which is predominantly between 140  $\mu\text{m}$  and 200  $\mu\text{m}$  in length, although some may reach 540  $\mu\text{m}$ . Egg sizes for small ST-2D shells may be around 140  $\mu\text{m}$  (only 2 data points available, after KNUDSEN, 1967; OLIVER & ALLEN, 1980b), suggesting lecithotrophic development; however, there is no evidence for any kind of brooding in Limopsidae (OLIVER & ALLEN, 1980b; HAIN & ARNAUD, 1992; MALCHUS & WARÉN, 2005; OLIVER & HOLMES, 2006).

Species of *Barbatia* GRAY, 1842, have either ST-2D or ST-3B shells, but some may also have ST-2A or 2B, judging from egg and P-1 sizes in MORAN (2004b), even though figures or P-2 dimensions were not given in that paper. Most species of *Acar* GRAY, 1857 in 1853–1857, possess a 3C type, and offspring in *Acar bailyi* BARTSCH, 1931 (determined as *Barbatia* in MORAN, 2004a, 2004b), develop from large eggs (160–225  $\mu\text{m}$ ) and are internally brooded to the juvenile stage. Typically, ST-2D shells do not surpass 200  $\mu\text{m}$ , whereas ST-3B and ST-3C shells vary between 210  $\mu\text{m}$  and 560  $\mu\text{m}$  (cf. LOOSANOFF & DAVIS,

1963; OLIVER & ALLEN, 1980a; MORAN, 2004a, 2004b).

The philobryid genera *Adacnarca* PELOSENEER, 1903; *Lissarca* E. A. SMITH, 1879; and *Philobrya* CARPENTER, 1873, have ST-3B ranging from 220  $\mu\text{m}$  to 1200  $\mu\text{m}$  and exceeding 500  $\mu\text{m}$  in length in most species. All philobryids examined by HAIN and ARNAUD (1992) brood their offspring in the mantle cavity. Sculptured shells correlate with an unattached development (D1/mc2 of HAIN & ARNAUD, 1992), whereas unsculptured larvae are enclosed by a vitelline membrane and connected by a navel cord to the visceral mass of the female (D2/mc1). *Adacnarca nitens* PELOSENEER, 1903, is an exception, however (own data).

Species of *Cratis* HEDLEY, 1915, and *Cosa* FINLAY, 1926, typically have ST-3C early shells, but some display transitional ST-2D/3B. Sizes range from ~190  $\mu\text{m}$  to 600  $\mu\text{m}$ , but in most species, early ontogenetic shells remain below 300  $\mu\text{m}$ . *Cosa waikikia* (DALL, BARTSCH, & REHDER, 1938) is an internal brooder that probably releases juveniles (HAYAMI & KASE, 1993). Hence, ST-3B and ST-3C of arcoids appear to correlate with extended internal brood protection and birth of juveniles. The assumed correlation between sculpture and brooding could not be tested.

### Pectinida

Pectinoids produce comparatively small eggs (45–180  $\mu\text{m}$ ) and prodissoconchs (Table 5). Species with an egg diameter of up to ~90  $\mu\text{m}$  are planktonic-planktotrophic (ST-2A; rarely ST-2B; e.g., LOOSANOFF, DAVIS, & CHANLEY, 1966; LE PENNEC, 1978). This holds true for all examined Pectinidae, except *Pseudohinrites levii* DIJKSTRA, 1989, which has medium or large eggs and a ST-2D shell measuring 170–180  $\mu\text{m}$  or 260  $\mu\text{m}$ , respectively. However, brooding has not been observed in this species (DIJKSTRA & KNUDSEN, 1997). Species of *Caribachlamys* WALLER, 1993, possess ST-2C shells measuring only 175–179  $\mu\text{m}$  in length, but egg sizes and development modes are unknown (WALLER, 1993).

Typical members of Propeamussiidae have a ST-2D larval shell reaching up to 220  $\mu\text{m}$ ,

but none with this shell type are known to brood. *Cycloclamys* FINLAY, 1926—until recently placed in Propeamussiidae, but now the type genus of Cyclochlamydidae (see DIJKSTRA & MAESTRATI, 2012)—differs from this pattern. *Cycloclamys tenuissima* (HAYAMI & KASE, 1993) has an intermediate ST-2D/3B larval shell and is a ctenidial brooder, whereas *C. incubata* (HAYAMI & KASE, 1993) has a ST-3C shell, broods supra-ctenidially and releases juveniles. *Cycloclamys* shells are ~240 µm to 300 µm long and microsculptured at release.

### Limida

Limoids are mainly characterized by ST-2A and ST-2D larval shells (Table 6); the ST-3C of *Limatula kinjoi* HAYAMI & KASE, 1993, seems to be a notable exception. *Limaria bians* (GMELIN, 1791 in 1791–1793) and *L. loscombi* (G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834) (ST-2A; P-1, ~80–90 µm, P-2, ~300–320 µm) are most likely planktonic-planktotrophic (LEBOUR, 1937; our data). It has not been confirmed whether *Limaria bians* protects its brood in a byssus nest (MERRILL & TURNER, 1963; HALL-SPENCER & MOORE, 2000).

ST-2D is typical of most species of *Limatula* S. V. WOOD, 1839 (egg size 130–150 µm), as well as of *Limea* BRONN, 1831; *Notolimea* IREDALE, 1924 (egg size 150 µm); *Ctenoides* MÖRCH, 1853 in 1852–1853; and some species of *Lima* BRUGUIÈRE, 1797 in BRUGUIÈRE & others, 1791–1827 (SALAS, 1994; LINSE & PAGE, 2003; MIKKELSEN & BIELER, 2003; ALLEN, 2004). *Limatula deceptionensis* PRESTON, 1916; *L. margaretae* ALLEN, 2004; and *Limea pygmaea* (PHILIPPI, 1845) with ST-2D brood in the mantle cavity (LINSE & PAGE, 2003; ALLEN, 2004).

Limoid ST-2D shells fall into two size classes: below 200 µm and between 200 µm and 440 µm. There is direct evidence for internal brooding in some species of the latter and one presumed instance in the former size class [*L. subovata* (JEFFREYS, 1876); ALLEN, 2004]. LINSE and PAGE (2003) speculated that the apparently nonbrooding

group has demersal eggs (cf. JÄRNEGREN, RAPP, & YOUNG, 2007).

### Ostreida

Pinnoidea appear to be largely planktonic-planktotrophic, and their shell type is correspondingly 2A (Table 7). However, few data are available for this group (SCHELTEMA & SCHELTEMA, 1984; ALLEN, 2011).

Similarly, all Pterioidea seem to develop from small eggs except for *Pulvinites exempla* (HEDLEY, 1914) (judging from the P-1 size). This species broods its offspring between the ctenidia and likely releases them as D-veligers (cf. TEMKIN, 2006). The shell belongs to type-2B, despite its unusually large P-1 of 290 µm.

Ostreioidea are mainly characterized by Shell Types 2A, 2B, and 3A (Table 8). Crassostreinae (Ostreidae) and possibly also Gryphaeidae exemplify planktonic-planktotrophic development from small eggs (35–62 µm for Crassostreinae) and a corresponding Shell Type 2A. However, available evidence for Gryphaeidae is indirect (Pycnodonteinae; see RANSON 1960, 1967; HARRY, 1985; MALCHUS, 1995). All members of the subfamily Ostreinae are internal brooders, brooding either between the ctenidia or in the mantle cavity. Yet, egg sizes may be as small as 60 µm, brooding time is short, and the shell is of type 2A [e.g., *O. puelchana* D'ORBIGNY, 1842; *O. permollis* (G. B. SOWERBY II, 1870b, 1871)]. Oysters with medium-large eggs (100–150 µm) develop ST-2B shells (e.g., *O. edulis* LINNAEUS, 1758). *Ostrea lutaria* HUTTON, 1873, and *O. chilensis* PHILIPPI, 1868, in KÜSTER & KOCH, 1843–1868, have large eggs between 200 µm and 310 µm and possess ST-3A shells. Larvae of *O. chilensis* have a functional velum and gut and are facultatively planktotrophic (CHAPARRO, THOMPSON, & WARD, 1993; CHAPARRO & others, 2001); they are released shortly before metamorphosis.

### Trigoniida and Unionida

Egg sizes and developmental modes are unknown for trigonioids. The single

description of an early shell of Recent *Neotrigonia* COSSMANN, 1912, suggests Shell Type 3B, but this classification requires confirmation (cf. Ó FOIGHIL & GRAF, 2000).

Unionoids are exceptionally well studied, except for the surprising scarcity of egg size data: these data have only rarely been reported. In one species of *Mutela* SCOPOLI, 1777, and one of *Alasmidonta* SAY, 1818, medium eggs measure ~180–190  $\mu\text{m}$  and large eggs measure 200  $\mu\text{m}$ , with corresponding glochidium sizes of 200  $\mu\text{m}$  and 270  $\mu\text{m}$ , respectively (FRYER, 1961, p. 261; CLARKE, 1981, p. 53). However, glochidium dimensions of 60  $\mu\text{m}$  to 150  $\mu\text{m}$  in Margaritiferidae and some Lampsilinae suggest much smaller and potentially yolk-poor oocytes. All unionoids have been grouped under Shell Type 4, and most of their trends were discussed in that section (p. 58, herein).

### Carditida

*Goodallia* TURTON, 1822 (Astartidae), and *Pteromeris* CONRAD, 1862 (Crassatellidae), have ST-2C shells, and the crassatellid *Salaputium* IREDALE, 1924, has a ST-2D shell (HAYAMI & KASE, 1993; GIRIBET & PEÑAS, 1999; new data for *Pteromeris*) (Table 9). Larval shells are around 200  $\mu\text{m}$ , except for one of four *Goodallia* species with a length of 329  $\mu\text{m}$ . Most egg sizes for *Astarte* J. SOWERBY, 1816 in 1812–1846, range from 110  $\mu\text{m}$  to 200  $\mu\text{m}$ , which would suggest a good correlation with the prodissoconch sizes measured for most other carditoids (<215  $\mu\text{m}$ ). These eggs are sticky and negatively buoyant, suggesting demersal development (OCKELMANN, 1959; SALEUDDIN, 1964, 1965, 1967; OERTZEN, 1972). However, according to LUTZ (1985, fig. 21B), *Astarte castanea* (SAY, 1822) has an egg diameter of ~310  $\mu\text{m}$  (~400  $\mu\text{m}$  including the gelatinous coat) and the enclosed P-1 is 254–264  $\mu\text{m}$  long. Brooding has not been observed in these carditoids.

Like crassatellids, Carditidae mainly produce 2C–2D shells that fall within two size classes, below 200  $\mu\text{m}$  and above 260

$\mu\text{m}$ ; the assignment of ST-2A to *Cardita kyushuensis* (OKUTANI, 1963) (= *C. uruma* HAYAMI & KASE, 1993) is tentative. Abundant evidence indicates internal brooding and release of juveniles in this group (DALL, 1903b; JONES, 1963; YONGE, 1969; SCHNEIDER, 1993; OLIVER & HOLMES, 2004; this study). According to JONES (1963), *Cyclocardia ventricosa* (GOULD, 1850a) develops in a brood chamber between the ctenidia, but details of the development and shell types of *Cyclocardia* CONRAD, 1867, are insufficiently known. *Cyclocardia borealis* (CONRAD, 1832) has an egg size of ~340  $\mu\text{m}$ , which encapsulates a P-1 or early D-veliger shell with a length of 264–286  $\mu\text{m}$  (LUTZ, 1985, fig. 21A); however, the developmental mode, hatching size, and shell type cannot be inferred. *Milneria kelseyi* DALL, 1916, and *Thecalia concamerata* (BRUGUIÈRE, 1792 in BRUGUIÈRE, LAMARCK, & DESHAYES, 1789–1832) are noteworthy, because they brood their offspring in an exterior ventral shell depression that is protected either by the periostracum (*M. kelseyi*) or by a deeply infolded shell wall (*T. concamerata*) (BRUGUIÈRE, 1792 in BRUGUIÈRE, LAMARCK, & DESHAYES, 1789–1832, p. 409; ABBOTT, 1954; YONGE, 1969, fig. 23).

Condylocardiidae are predominantly characterized by early ontogenetic Shell Types 2D and 3C, with a strong taxonomic division within the family. Shell Type 3C is typical of *Benthocardiella* POWELL, 1930, *Condylocardia* BERNARD, 1896c (both Condylocardiinae), and *Condylocuna* IREDALE, 1936 (Cuninae), whereas *Crassacuna* MIDDELFART, 2002b (Cuninae) is characterized by ST-2D and *Warrana* LASERON, 1953 (Cuninae) has types 2D and some ST-2C. There is rather convincing evidence that shell types based on ST-3C are correlated with internal brooding to the juvenile stage. However, except for *Condylocardia notoaustralis* COTTON, 1930, which keeps its brood in the supra-ctenidial chamber, specific knowledge of brooding modes in this family is lacking (MIDDELFART, 2002a, 2002b).

### Lucinida

Larval shells of Lucinidae are poorly known (Table 10). *Codakia orbicularis* (LINNAEUS, 1758) develops externally within a negatively buoyant, nonsticky egg; the larva hatches as a D-veliger (ALATALO, BERG, & D'ASARO, 1984; GROS, FRENKIEL, & MOUËZA, 1997) with the final larval shell being of type 2C and measuring up to 200  $\mu\text{m}$ . *Lucinoma aequizonata* (STEARNS, 1890) has positively buoyant eggs (yolk mass diameter of 200  $\mu\text{m}$ ; with a jelly coat measuring 500  $\mu\text{m}$  in diameter). Offspring hatch as D-veligers of  $\sim 240$   $\mu\text{m}$ , probably including the early P-2 shell, but the final size and type of the larval shell are unknown (GROS, DUPLESSIS, & FELBECK, 1999). *Phacoides pectinatus* (GMELIN, 1791 in 1791–1793) produces a gelatinous egg case with several jelly-coated eggs in which offspring develop to an advanced D-veliger stage and hatch shortly before metamorphosis (ST-2D,  $\sim 200$   $\mu\text{m}$ ; COLLIN & GIRIBET, 2010).

All examined Thyasiridae have early shells of the 2D type, most of which are less than 200  $\mu\text{m}$  in length (maximum length 270–300  $\mu\text{m}$ ) (OLIVER & KILLEEN, 2002; BARRY & MCCORMACK, 2007). Brooding has not been observed in this group even though PAYNE and ALLEN (1991, p. 486) mention lateral brood pouches for the genus *Thyasira* LAMARCK, 1818 in 1818–1822.

### Cardiata

Cardioidea and Tellinoidea seem to be predominantly of Shell Type 2A; eggs are shed into the water, some apparently with a jelly coat, and development may advance until the D-veliger before hatching (OCKELMANN, 1959; CHANLEY, 1969; OERTZEN, 1972; FRENKIEL & MOUËZA, 1979; HAYAMI & KASE, 1993; HENDRIKS, DUREN, & HERMAN, 2005). *Goethemia elegantula* (BECK in MØLLER, 1842) seems to be the only brooding cardiid (in a brood pouch formed by the ventral mantle margin). The reported shell size of  $\sim 1200$   $\mu\text{m}$  at hatching and the apparent existence of an inner boundary at  $\sim 530$   $\mu\text{m}$  indicates that offspring are released

as juveniles (MATVEEVA, 1953; SCHNEIDER, 1998, fig. 12, 23N) (see discussion under Shell Type 3C, p. 56, herein).

Veneroidea, Arcticoidea, and Galeommatoida (among other superfamilies) are more variable, commonly developing early ontogenetic Shell Types 2A and 3A (Table 11). In Galeommatoida, Shell Type 2A is typically related to internal brooding between and dorsal to the ctenidia, and larvae are released as D-veligers. Egg sizes are mostly small ( $<80$   $\mu\text{m}$ ) and the P-1 is  $\sim 100$ – $155$   $\mu\text{m}$  long. Nevertheless, posthatch growth is considerable, so that the P-1/P-2 ratio stays below 0.5 (hence, ST-2A). Some Galeommatoida possess ST-3A. Where known, this type is related to internal brooding until the juvenile stage. The veneroidean *Turtonia minuta* (FABRICIUS, 1780), however, broods its offspring in an egg clutch attached to the byssus of the female (Shell Type 3A is inferred from OCKELMANN, 1964, p. 136; see also OLDFIELD, 1955). The neoleptonid *Lutetina capricornia* OLIVER & HOLMES, 2004, is characterized by ST-3B (see also Ó FOIGHIL, 1986, 1989; MIKKELSEN & BIELER, 1989, 1992; SALAS & GOFAS, 1998; Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999; COSEL & SALAS, 2001; FOX, JESPERSEN, & LÜTZEN, 2007; ITUARTE, 2009; PARK & CHUNG, 2004; PASSOS & DOMANESCHI, 2009; among others).

### Pholadata

The families Xylophagidae (see DISTEL & others, 2011) and Teredinidae develop predominantly ST-2A (Table 12), which correlates with small eggs ( $<80$   $\mu\text{m}$ ) and brooding at least to the D-veliger stage. Some teredinids develop matrotrophically in ctenidial brood pouches and are released as competent P-2-veligers (SHIPWAY, 2012), but their egg size and shell characters are indistinguishable from ST-2A of planktonic-planktotrophic species. In numerous species of Xylophaginae and Teredinidae, dwarf males attach within the mantle cavity or externally to the posterodorsal shell margin (TURNER & YAKOVLEV, 1983; HAGA & KASE,



2010). Their shells are externally indistinguishable from brooded larvae, suggesting that many older descriptions of larvae may actually refer to dwarf males (KNUDSEN, 1961). However, observations of Xylophaginae indicate that the inner shell layer of dwarf males is tubulated, crossed lamellar, and has well-defined muscle scars (present observations), which are typical postmetamorphic shell characters. Note that dwarf males are also common in Galeommatoidea (see TURNER & YAKOVLEV, 1983, and references therein; MACKIE, 1984).

### Anomalodesmata

Larval shells in the megaorder Anomalodesmata (e.g., Poromyoidea, Cuspidarioidea, Verticordioidea, Pandoroidea, Clavagelloidea, Thracioidea, Pholadomyoidea, and, in part, the Anomalodesmata of authors) appear to be mainly of type 2C and 2D (Table 12). As far as known, most Anomalodesmata have eggs individually encased in a negatively buoyant, multilayered jelly coat. In most families, they range from 100  $\mu\text{m}$  to <200  $\mu\text{m}$  (OCKELMANN, 1959, 1965; ALLEN, 1961; KNUDSEN, 1967; KUBO, ISHIKAWA, & NUMAKUNAI, 1979; CAMPOS & RAMORINO, 1981; SARTORI & DOMANESCHI, 2005; among others), but evidence available for Pholadomyoidea and Parilimyioidea, albeit limited, suggests somewhat smaller sizes: 60–85  $\mu\text{m}$  ymd in *Pholadomya candida* G. B. SOWERBY I, 1823 in 1821–1828, 1831–1834) and 70  $\mu\text{m}$  in *Parilimyia fragilis* (GRIEG, 1920) (MORTON, 1980, 1982).

Among the remaining Anomalodesmata, the thracioidean *Thracia phaseolina* (LAMARCK, 1818 in 1818–1822) has an exceptionally small egg with a yolk mass diameter of ~55  $\mu\text{m}$  and larval Shell Type 2A (OCKELMANN, 1965, fig. 3; present observations, 2008). The pandoroidean *Laternula elliptica* (KING & BRODERIP, 1832) (ST-2C) was reported to have egg sizes of 200–220  $\mu\text{m}$  (BERKMAN, WALLER, & ALEXANDER, 1991; PECK, POWELL, & TYLER, 2007), but its yolk mass diameter is in the range of 120–150  $\mu\text{m}$  (KANG, AHN, & CHOI, 2009).

The most common mode of development in megaorder Anomalodesmata seems to be nonbrooded, taking place, at least initially, within negatively buoyant capsules. Hatching may occur during the trochophore, as, for example, in *Pandora inaequivallis* (LINNAEUS, 1758) (ALLEN, 1961) and possibly, in *Entodesma cuneata* (GRAY, 1828) (CAMPOS & RAMORINO, 1981), allowing for a demersal or planktonic larval period. In some instances, hatching may be delayed until the early juvenile phase: in *Cardiomya pectinata* (CARPENTER, 1864) and *Laternula elliptica* (KING & BRODERIP, 1832) (GUSTAFSON, Ó FOIGHIL, & REID, 1986; PECK, POWELL, & TYLER, 2007). Brooding of embryos, larvae, or juveniles seems rare and has only been recorded in *Thracia myopsis* MÖLLER, 1842 (OCKELMANN, 1965), *Lyonsia arcaeforme* MARTENS, 1885 (HAIN & ARNAUD, 1992), and *Grippina californica* DALL, 1912 (COAN, 1990).

### Solenata

Limited data are currently available for members of the megaorder Solenata (superfamilies Solenoidea and Hiatalloidea), which indicate a 2A and 2B larval Shell Type (Table 13). All species are oviparous, and solenid eggs may have a jelly coat [OCKELMANN, 1959; LOOSANOFF & DAVIS, 1963; BREESE & ROBINSON, 1981; HAYAMI & KASE, 1993; CHUNG & others, 2008; COSTA, DARRIBA, & MARTÍNEZ-PATIÑO, 2008; COSTA & MARTÍNEZ-PATIÑO, 2008; present shell data for *Hiatella arctica* (LINNAEUS, 1767 in 1766–1767)].

## DEVELOPMENT AND SHELL TRENDS: CONCLUSIONS

Direct measurement of egg energy content within the Bivalvia is a pending and indispensable task for assessing developmental hypotheses. However, we did not find marked differences between protobranch and autobranch yolk masses, assuming that both groups are lecithotrophic during the P-1 larval phase. We saw no reason for hypothesizing different energy/mass ratios in

TABLE 17. Summary of the developmental characters related to shell types. Parentheses indicate rare occurrence; question marks indicate evidence is lacking; *ST*, shell type; *ymd*, yolk mass diameter; *L*, large ( $\leq 300 \mu\text{m}$ ); *M*, medium/large ( $\leq 200 \mu\text{m}$ ); *S*, small ( $\leq 90 \mu\text{m}$ ); *XL*, very large ( $> 300 \mu\text{m}$ ); nutrition: *lec*, lecithotrophic; *mat*, matrotrophic; *mix*, mixotrophic; *par*, parasitic; nonbrooding: *be*, benthic; *pl*, planktonic; release type: *av*, advanced veliger; *dv*, D-veliger; *j*, juvenile; *ml*, metalarva (new).

ST	ymd	Nutrition	Nonbrooding	Brooding	Release type
1	S-L	lec	be, pl	in some	?ml, j
2A	S, M	mix (mat)	pl, be	in some	dv, (av)
2B	M	mix	pl, be	yes, except ratios 0.6–0.7	dv
2C	M, L	mix	?	rare, not between ratios 0.75–0.9	j
2D	M	lec	be, ?pl	common	av, j
3A	L	lec	no	all	av, j
3B	L, XL	lec	no	all	j, ?av
3C	L	lec	no	all	j, ?av
4	?S, M-L	mix (mat+par)	no	all and parasitic	larva, + j

this case. In both taxa, over 90% of the eggs (*ymd*) are smaller than  $200 \mu\text{m}$ ; the medians for the overlapping range between  $70 \mu\text{m}$  and  $200 \mu\text{m}$  are almost the same ( $134 \mu\text{m}$  versus  $126 \mu\text{m}$ ), and they are identical for the range from  $70 \mu\text{m}$  to  $300 \mu\text{m}$  ( $138 \mu\text{m}$ ).

Yolk mass diameters can be grouped into small ( $\leq 90 \mu\text{m}$ ), medium/large ( $\leq 200 \mu\text{m}$ ), large ( $\leq 300 \mu\text{m}$ ) and very large ( $< 600 \mu\text{m}$ ). Although small eggs are overall correlated with planktotrophic development (during the autobranch P-2 phase), the tripartite distinction into planktotrophic-long planktonic, lecithotrophic-short planktonic, and direct (Table 1) does not reflect developmental modes well. Brooding and brooding time in marine autobranchs can be freely combined with any egg size and is sometimes combined with matrotrophy, which cannot be inferred from egg size (e.g., Teredinidae, Unionidae). Parental care in nonbrooding species is represented by the production of gelatinous coated eggs, and this protective layer occasionally co-occurs with internal brooding. Overall, such modulation is likely to have repercussions on egg size, leading to rather broad transitional zones and complex relationships among *ymd*, dependence on exotrophy, and P-1 size. Therefore, it is not surprising that the present shell typology captures more morphological differences than can be detected comparing *ymd* and P-1 size ranges statistically (Fig. 41.1–41.2).

Table 17 summarizes key developmental characters related to shell types. Protobranch developmental modes are still too poorly known to reveal possible correlations with Shell Types 1A to 1C. It also remains unclear whether brooded offspring could be released as competent larva or shortly after metamorphosis without nepioconch growth (together referred to as metalarva in Table 17), instead of always as a juvenile with nepioconch growth.

In marine autobranchs, Shell Type 2A is highly correlated with small egg sizes ( $25\text{--}90 \mu\text{m}$ ) and extended exotrophy (including matrotrophy), but the overall shell morphology is the same for brooding and nonbrooding species, except for the statistically significant difference in P-1 size (Fig. 43.4). Shell Types 2B to 2D cannot be distinguished on the basis of their medium/large eggs. However, a strange gap occurs in the range of P-1/P-2 ratios, corresponding to the upper 2B and most of the 2C partitions, which lack brooding taxa and could indicate a benthic or planktonic developmental mode.

Similarly, many species with Shell Type 2D have never been observed to brood (e.g., Limidae, Limopsidae). All ST-3 shells derive from large to very large eggs (Table 2); the yolk mass diameters (*ymd*) also seem to differ for ST-3A to ST-3C, but too few observations are currently available, which hampers statistical treatment (Table 2).

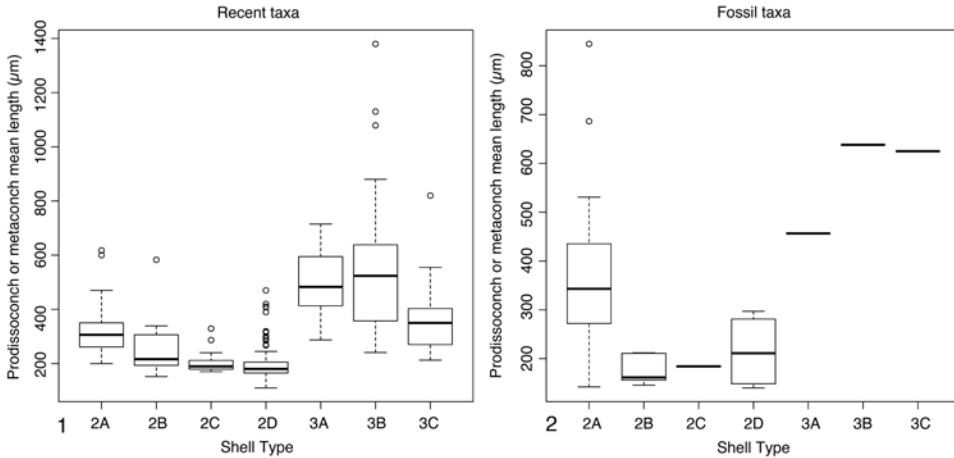


FIG. 44. Boxplots of P-2 mean sizes in 1, Recent and 2, fossil Autobranchia (excluding Unionida), grouped according to Shell Types 2A to 3C; number of observations. 1, 2A = 100, 2B = 16, 2C = 28, 2D = 117, 3A = 10, 3B = 24, 3C = 30; 2, 2A = 31, 2B = 6, 2C = 2, 2D = 4, 3A = 1, 3B = 1, 3C = 1 (new).

Brooding species with ST-2A to ST-2C most commonly release D-veligers that still require a free larval phase to reach metamorphic competence. All species with ST-2D appear to become competent without exotrophic feeding, whether brooded or not, and are normally released as competent larvae, rarely as a juvenile. Species with ST-3A release advanced veligers, and probably all species with ST-3B and 3C release juveniles. Shell Type 4 refers to unionids which are probably all lecithotrophic, matrotrophic, and parasitic. Unfortunately, egg sizes are largely unknown and shells must be presently considered as cryptoconchs. Thus, trends in egg and prodissoconch sizes could not be examined in this group.

Figure 44.1 shows the ranges of final early ontogenetic shell sizes for Recent marine autobranchs, which is essentially identical to the distribution chart including fossil taxa (Fig. 34). In ST-2A to 3A, the size corresponds to the larval shell, and in ST-3B and 3C to the metaconch or cryptoconch (assumed to be postlarval as well). Overall ranges group shell types into the ST-2 series and ST-3 series, respectively. A recurrent theme is the median close to 200 µm for Shell Types 2B to 2D (as detailed in the

section above on Taxonomic Patterns in Recent Autobranchia, p. 76). That section also reveals a strong taxonomical bias in the distribution of shell types (Tables 3–13), which requires further analysis.

### FOSSIL RECORD

Early ontogenetic shells of fossil bivalves have been described from relatively few and stratigraphically rather disjunct units. However, many fine siliciclastic and carbonaceous-siliciclastic sediments from the Jurassic to the Holocene yield well-preserved material.

The Cambrian *Pojetaia runnegari* JELL, 1980 (RUNNEGAR, 2007) represents one of the most basal bivalve groups currently recognized. The shape and dimensions of its early ontogenetic shell compare best with modern protobranchs showing Shell Type ST-1A or ST-1B. The P-1 measures ~175 µm and the presumed nepioconch ~260 µm in length (inferred from RUNNEGAR, 2007, fig. 1). Some early ontogenetic shells of post-Paleozoic protobranchs were shown in LABARBERA (1974), LA PERNA (2003, 2007a, 2007b), LA PERNA, CEREGATO, and TABANELLI (2004), and KIEL (2006). Of the Eocene-Oligocene protobranchs described

by KIEL (2006), *Tindariopsis* cf. *grasslei* (ALLEN, 1993) has the same characteristic P-1 sculpture and similar, though smaller, size (220  $\mu\text{m}$ ) as its Recent counterpart. The alleged P-2 of ~500  $\mu\text{m}$  of the Oligocene *Ledella* sp. (KIEL, 2006) represents the nepioconch; the P-1 measures 125–135  $\mu\text{m}$ . The true P-1 size (108  $\mu\text{m}$ ) of “*Tindaria*” sp. may be somewhat larger, as much of the shell is hidden below a sediment cover. All shells conform well to ST-1(A or B).

Silurian and Devonian Cyrtodontida, Pteriomorpha, have a typical ST-2A larval shell with a P-1 between 75  $\mu\text{m}$  and 120  $\mu\text{m}$  and a P-2 stage of ~220  $\mu\text{m}$  to 1200  $\mu\text{m}$  (see DZIK, 1994, cyrtodontids, pl. 31, 32, 36; KŘÍŽ, 1979, cardioids, pl. 10,2–3). In other Silurian to late Carboniferous (Pennsylvanian) Pteriomorpha, the visible early shell could also belong to the nepioconch stage and the P-1 size cannot be estimated in these instances (e.g., KŘÍŽ, 1966, 1996b, 1998; YANCEY & HEANEY III, 2000). Most of these early shells are very large (~1400–2400  $\mu\text{m}$ ), but this does not exclude them from representing prodissoconch-2 stages (see also NAGEL, 2006).

Jurassic-Cretaceous and most Tertiary-Quaternary pteriomorphs have ST-2A, including parallelodontids, an Upper Cretaceous *Striarca* CONRAD, 1862 (Arcida), and a Tertiary *Idas* JEFFREYS, 1879 (Mesozoic: LUTZ & JABLONSKI, 1978b; KEMPER, 1982; MALCHUS, 1995, 2004a, and references therein; KIEL, 2004; KOPPKA & MALCHUS, 2007; Tertiary, Quaternary: BERNARD, 1898; MALCHUS, 1995; KIEL & GOEDERT, 2007; GLAWE & others, 2011; see also below). Noteworthy exceptions include a Pleistocene ostreoid, *Ostrea chilensis* PHILIPPI, 1868, in KÜSTER & KOCH, 1843–1868 (Ó FOIGHIL & others, 1999), with ST-3A, and two philobryids: *Cosa wanganuica* FINLAY, 1930, with ST-3B (BEU & MAXWELL, 1990) from the Pleistocene, and Eocene *Limarca* TATE, 1886, with ST-3C according to the description by TEVESZ (1977).

Early ontogenetic shells from fossil Unionida, Palaeoheterodonta, are unknown.

A single undetermined Trigoniida from the Middle Jurassic has a typical ST-2B shell (present data, herein) [cf. Recent *Neotrigonia margaritacea* (LAMARCK, 1804) with questionable ST-3B (Ó FOIGHIL & GRAF, 2000)]. No other juvenile Trigoniida from the Jurassic that preserve the larval shell or its inner mold have been described.

Early ontogenetic shells of Cardiata, Archiheterodonta, are known from Jurassic astartids: *Nicaniella* CHAVAN, 1945; *Oxyeurax* GARDNER & CAMPBELL, 2007 (replacement name for *Oxyloma* GARDNER & CAMPBELL, 2002); *Pressastarte* ZAKHAROV, 1970, with ST-2B and ST-2D; Upper Cretaceous *Uddenia texana* STEPHENSON, 1941, with ST-2A; and *Vetericardiella crenalirata* (CONRAD, 1860), with ST-2C (JABLONSKI & LUTZ, 1980, fig. 10A,B; see also JABLONSKI & LUTZ, 1983, fig. 2C–D), an Eocene *Crassinella* GUPPY, 1874, species (ST-2C), and Miocene-Pliocene *Crassatellites* (*Crassinella*) *dupliniana* DALL, 1903a (ST-2B) (LABARBERA, 1974; KOPPKA & MALCHUS, 2007; and *Oxyeurax* sp., herein). The Early Miocene *Cuna* HEDLEY, 1902, “n. sp.” (*Volupicuna* IREDALE, 1936, “n. sp.” of BEU & MAXWELL, 1990) has a ST-2D. Several other condylocardiid genera have been described from Tertiary rocks of New Zealand, but their early ontogenetic shell types are not known.

Within Euheterodonta, Lucinata, Early Triassic *Sinbadiella pygmaea* HAUTMANN & NÜTZEL, 2005 (Lucinidae) exhibits a ST-2A (P-1 < 100  $\mu\text{m}$ ; P-2 ~260  $\mu\text{m}$ ; inferred from fig. 2F in HAUTMANN & NÜTZEL, 2005). A Miocene species of *Parvilucina* DALL, 1901, has a ST-2C shell measuring 200  $\mu\text{m}$  in length (LABARBERA, 1974), and *Thyasira xylochia* KIEL & GOEDERT (2007) (Thysiridae) from the Eocene-Oligocene has a ST-2D shell (KIEL & GOEDERT, 2007, fig. 7C).

Within Cardiata and Solenata, the oldest known early ontogenetic shells belong to Silurian *Butovicella* KŘÍŽ, 1965 (Modiomorphida, Cardiata), at least some species of which possess a ST-2A shell (KŘÍŽ, 1969, pl. 1, 1, 4; pl. 4, 6; DZIK, 1994, fig. 32G; see also

refigured specimens in MALCHUS, 2004b, fig. 6E,F,H). The Middle Jurassic *Myoconcha crassa* J. SOWERBY, 1824 in 1812–1846 (KAIM & SCHNEIDER, 2012) (Cardiida, Cardiata) has a ST-2D (240  $\mu\text{m}$ ) surrounded by a shell collar, which is presently interpreted as the early nepioconch, extending the overall early ontogenetic shell size to 360  $\mu\text{m}$ . The Middle Jurassic *Hiatella phaseolus* (EUDES-DESLONGCHAMPS, 1838) (SCHNEIDER & KAIM, 2012) (Hiatellida, Solenata) has a ST-2A that is similar in shape and size to Recent species of *Hiatella*, and the Late Pliocene *Neolepton antipodum* (FILHOL, 1880) (Cardiida, Cardiata) has a ST-2D shell (BEU & MAXWELL, 1990, pl. 52).

## EVOLUTIONARY PERSPECTIVES

Significant gaps still exist in our knowledge of developmental types in living bivalves, their correlation with shell types, autecologic and synecologic factors, and especially their geologic history. Thus, the following summary presents questions that surfaced during the preparation of this chapter in the hope of encouraging future inquiry.

### ANCESTRAL CHARACTER STATES

Comparisons with Recent protobranchs suggest that Cambrian Euprotobranchia were lecithotrophic, though this is based on observations of a single species, *Pojetaia runnegari*. As in Recent protobranchs, the assumed ST-1A (or 1B) of *Pojetaia* provides no clues to infer brood protection. Similarly, it is not evident from the shell morphology that the plesiomorphic larval type was a pericalymma, rather than a trochophore from which pericalymma and veliger could have evolved either sequentially or independently. A better understanding of the transition from Cambrian euprotobranchs to the Ordovician radiation—the roots of most major bivalve lineages—is needed. It appears reasonable, though, to assume that Paleozoic Protobranchia developed through

a pericalymma larva and that the early shell consisted of a prodissoconch-1 (primary absence of a P-2), and the postlarval nepioconch. The early hinge and ligament evolution remain unknown in this group.

Limited evidence from Paleozoic Autobranchia suggests that Silurian and Devonian Cyrtodontida (Pteriomorphia) and Silurian Butovicellinae (Modiomorphida, Cardiata) had type 2A shells, which would indicate development from veliger larvae. It is hypothesized that this type of larva, together with the larval tooth generation G1, is plesiomorphic for all Autobranchia (see previous discussion under the section Homology of Tooth Series, p. 49, and the next section, herein).

### EVOLUTION OF LECITHOTROPHY AND PLANKTOTROPHY

The early evolution of bivalve larval nutrition is still a contentious issue, which is largely based on conjecture (JABLONSKI & LUTZ, 1983; RUNNEGAR, 2007; VALENTINE & JABLONSKI, 2010; see also section below on Developmental Modes Along Latitudes, p. 89–90, herein). Reviewing all arguments on present knowledge—including outgroups—appears futile, and so the following discussion is restricted to Bivalvia.

Based on comparison with Recent bivalves, it is reasonable to assume that, regardless of their larval type, early Cambrian *Pojetaia* was fully lecithotrophic if it metamorphosed at the end of the P-1 larval phase. If it developed from a pericalymma, the P-1 size of ~175  $\mu\text{m}$  might be a poor estimator of egg size, as discussed previously (note that shell length is derived from measurements of fig. 1 in RUNNEGAR, 2007, following the indication for the P-1 boundary). However, the specimen figured by RUNNEGAR (2007) has a second, weakly delimited shell boundary at ~260  $\mu\text{m}$  that could represent a prodissoconch-2. If so, the larval shell would be similar to ST-2B (P-1/P-2 ratio 0.67) and larval nutrition was most likely mixotrophic. This ratio is higher than the P-1/nepioconch ratios calculated for five Recent and one

Jurassic protobranchs (0.24–0.53), but current knowledge is insufficient to draw any conclusions. Hence, no convincing argument can be made to support inferences of the nutritional regime of early Cambrian bivalves on the basis of shell morphology.

The first convincing indication of mixotrophy is provided by the ST-2A shells of Silurian Cyrtodontida and Modiomorphida, so that one may assume that planktotrophy (rather than matrotrophy) evolved in those clades in the Ordovician or Silurian. Whether this developed independently in the two taxa is unknown. The P-2 shells of some cyrtodontids measure ~600 µm to 1100 µm (DZIK, 1994), which contrasts with cardiolid Cyrtodontida of up to 300 µm (KŘÍŽ, 1979), suggesting that the exotrophic phase may have been longer than in the latter group.

Trigoniida and the cardiomorph Astartidae (Carditida) and Kalenteridae (Cardiida) had larger P-1 sizes and probably medium/large eggs since at least the Middle Jurassic (ST-2B, 2C, 2D) or possibly since their appearance in the Paleozoic. The Cretaceous crassatellid *Uddenia texana* STEPHENSON, 1941, and the Tertiary crassatellid *Crassatellites* (*Crassinella*) *duplinianus* DALL, 1903a, are characterized by Shell Types 2A and 2B, respectively, which may indicate increased dependence on lecithotrophy and a change of developmental mode (for shell characters, see JABLONSKI & LUTZ, 1980; HAYAMI & KASE, 1993; for *Pteromeris* CONRAD, 1862, see Table 9). A similar change occurred between early Triassic and Recent Lucinida, which exhibit ST-2A and ST-2C to 2D, respectively.

All egg sizes related to Shell Type 3 in living bivalves indicate fully lecithotrophic development. Hence, ST-3B and ST-3C in Eocene Philobryidae (Arcida, Pteriomorpha) and Condylcardiidae (Carditida, Archiheterodonta) indicate development from large to very large yolky eggs (Fig. 44.2). In Ostreoidea, Shell Type 3A and, thus, yolk-rich eggs are unknown before the Pleistocene. All other fossil ostreoids known

so far from the Early Jurassic to the Eocene were yolk-poor (ST-2A) (MALCHUS, 1995, 2004a; GLAWE & others, 2011; J. KOPPKA, personal communication, 2007). Hence, lecithotrophic-planktotrophic or fully lecithotrophic oysters may not have evolved before the late Eocene or Miocene.

These patterns could indicate a general evolutionary trend from planktotrophic to nonplanktotrophic development in autobranch bivalves once the (feeding) veliger larval type had evolved (see HASZPRUNAR, SAVINI-PLAWEN, & RIEGER, 1995, for a discussion on the oldest molluscan larval type). If so, the transition probably occurred independently in many lineages and at different times. This is comparable to hypotheses for other invertebrate groups (see JABLONSKI & LUTZ, 1983, for a review and older references; STRATHMANN, 1985, 1993; JEFFERY & EMLET, 2003), but fossil evidence from bivalves is still too scanty for a meaningful comparison.

#### EVOLUTION OF BROODING

Current data on egg size, P-1 size, and P-1/P-2 ratios from Recent bivalves suggest that brooding and lecithotrophy are not strictly correlated and that brooding occurs in combination with all autobranch shell types. However, the brooding gap for ST-2B and ST-2C could indicate planktonic or demersal development, as hypothesized for limids and limopsids with ST-2D (LINSE & PAGE, 2003; MALCHUS & WARÉN, 2005). Shell Types 2A to 2D alone are not a sufficient basis for inferring larval dispersal capacity (see DIJKSTRA & GOFAS, 2004, p. 73, for a recent example). However, shell types and developmental modes show a strong taxonomical distribution (see above) that can be used to reduce the uncertainty of inferences.

These limitations do not apply to ST-3, which, as far as currently known, always indicates long-term (and probably) internal brooding. The mode of development first appears in the fossil record in Eocene Philobryidae (Arcida) and Cuninae (Carditida).

There is no evidence for inferring the same type of shell and mode of development in the Triassic, putative philobryid *Eophilobryoidella* (STILLER & CHEN, 2004).

### MINIATURIZATION

Most literature data on living species suggest that long-term brooding and Shell Types 3B and 3C are correlated with small adult sizes: ~5 mm and often smaller than 3 mm (e.g., LASERON, 1953; JABLONSKI & LUTZ, 1983; BEU & MAXWELL, 1990; HAYAMI & KASE, 1993; MIDDELFART 2002a, 2002b; MORAN, 2004a; OLIVER & HOLMES, 2004; BEU & RAINE, 2009). This is especially obvious in some Arcidae (e.g., *Acar, Barbatia*), Philobryidae, and Condylorcardiidae. It is also true for *Cyclochlamys incubata* (HAYAMI & KASE, 1993) (Cyclochlamydidae), *Carditella pileolata* (OLIVER & HOLMES, 2004) (Carditidae), and, by inference, probably also *Limatula kinjoi* HAYAMI & KASE (1993) (Limidae).

There are exceptions, as demonstrated by *Ostrea chilensis* PHILIPPI, 1868, in KÜSTER & KOCH, 1843–1868 (ST-3A combined with larger adult size), Teredinidae (ST-2A, small adult shell but large body size, and larval sized dwarf males), or small Lasaeidae (ST-2A, 3A), and Crenellinae (ST-2D) (e.g., Ó FOIGHIL, 1986, 1989; SALAS & GOFAS, 1997; Ó FOIGHIL & others, 1999; Ó FOIGHIL & THIRIOT-QUIÉVREUX, 1999; SHIPWAY, 2012). However, we suspect that ST-3B and ST-3C (but not ST-3A) develop when the brood is retained until after metamorphosis, which is consistent with our distinction between prodissoconch, metaconch, and cryptoconch.

The available evidence from the fossil record suggests that miniaturization in combination with ST-3B and ST-3C appeared in the Tertiary (?Eocene), at least in Arcida and Carditida. It is obvious, however, that long-term brooding alone cannot explain this apparent evolutionary trend. Other life-history traits likely to influence shell type are specific brood location (HAIN & ARNAUD, 1992), availability of

brood space, ctenidial structure, physiological factors, and tradeoffs between egg size (and energy content) and fecundity, among others. The task of linking and interpreting all available data remains to be accomplished (for earlier references, see JABLONSKI & LUTZ, 1983).

External ecological factors probably also play an important role in miniaturization and brooding duration. Cold ambient temperatures might favor ST-3B, whereas mild to warm ambient temperatures might favor ST-3C (cf. Philobryidae and Carditida from the Antarctic to Japan; DELL, 1964, 1990; BEU & MAXWELL, 1990; HAYAMI & KASE, 1993; MIDDELFART, 2002a, 2002b). However, as discussed below, water depth and light conditions do not appear to be controlling factors (MALCHUS & LINSE, unpublished data on water depth, 2004; personal data on Philobryidae and Carditida, 2004).

Miniaturization and brooding often co-occur with reduced development of the hinge, ligamental structures, and ctenidia. Such reductions have been usually attributed to heterochronic processes (mostly termed neoteny in the older literature), but these have yet to be analyzed in detail (e.g., BERNARD 1896d, 1897; OCKELMANN, 1964; SALAS, 1994; GOFAS & SALAS, 1996; EVSEEV, KOLOTUKHINA, & SEMENIKHINA, 2007).

### DEVELOPMENTAL MODES IN THE DEEP SEA

Deep-sea bivalves commonly cope with different environmental conditions from their shallow-water counterparts, which include differences in ambient pressure, temperature, oxygen levels, water chemistry, light, seasonality, and type of food. These environmental differences correlate with decreased diversity of higher taxa and increased dominance of certain protobranch and autobranch families (Atlantic Ocean: ALLEN, 2008; Southern Ocean: LINSE & others, 2006; BRANDT & others, 2007; BRANDT, LINSE, & SCHUELLER, 2009). Wood falls (KNUDSEN,

1961; VOIGHT, 2009), whale falls (BACO & SMITH, 2003; TYLER & others, 2009), hydrothermal vents, and cold seeps provide special physical-chemical conditions and community structures (OLU-LE ROY & others, 2004; SASAKI, OKUTANI, & FUJIKURA, 2005; JÄRNEGREN, RAPP, & YOUNG, 2007; GÉNIO & others, 2008; VRIJENHOEK, 2009); see reviews in KIEL (2010) and also KIEL and LITTLE (2006) and KIEL and GOEDERT (2007).

One might expect that the unique environmental factors of the deep sea led to distinctive modes of development, but early ontogenetic shells so far provide only limited evidence. Further in-depth studies are needed before generalizations can be made. No argument can presently be constructed to explain the increasing proportion of Nuculanidae and Yoldiidae at greater depths (cf. ALLEN, 2008). All protobranchs are presumably lecithotrophic—hence, excluding matrotrophy and feeding on dissolved organic matter—but descriptions of their development and larval shells are anecdotal (e.g., ALLEN, 1993; OCKELMANN & WARÉN, 1998; SCHELTEMA & WILLIAMS, 2009; BENAÏM, VIEGAS, & ABSALÃO, 2011). Protobranch dominance in the deep sea may simply reflect the vastness of organic-rich bottom sediments that favor deposit-feeding bivalves, or their hemocyanin or hemoglobin may have preadapted them to oxygen-depleted environments (MANGUM & others, 1987; ALLEN, 1993; TAYLOR, DAVENPORT, & ALLEN, 1995; ANGELINI & others, 1998; SANDERS, CHILDRESS, & MCMAHON, 1998).

Among autobranch families ranging from subtidal to abyssal or even hadal depths, the Limopsidae, Propeamussiidae, Thyasiridae, Cuspidariidae, and the majority of Limidae are characterized by ST-2D, which may indicate benthic as well as pelagic lecithotrophic development; none has been found to brood. All philobryids appear to be long brooders with ST-3B or ST-3C. In contrast, deep-sea pectinids (possibly present only in waters shallower than 2000 m) possess predominantly ST-2A. Species lists with

depth ranges are given by PAYNE and ALLEN (1991), OLIVER and KILLEEN (2002), DIJKSTRA and GOFAS (2004), OLU-LE ROY and others (2004), JÄRNEGREN, RAPP, and YOUNG (2007), ALLEN (2008), BRANDT, LINSE, & SCHUELLER (2009, fig. 4), and DIJKSTRA and MAESTRATI (2012).

Xylophagids are the most typical colonizers of wood falls, at least down to 7000 m. Unfortunately, the distinction between brooded offspring and dwarf males, as well as the differences between shell types of brooded and nonbrooded larvae, are still largely unresolved (KNUDSEN, 1961, 1967; CULLINEY & TURNER, 1976; TURNER, 2002; PAILLERET & others, 2007; TYLER, YOUNG, & DOVE, 2007; VOIGHT, 2009; HAGA & KASE, 2010; OCKELMANN & DINESEN, 2011; VOIGHT & SEGONZAC, 2012). It would not be surprising, therefore, if both nonbrooded and brooded larvae had planktotrophic-like shells (ST-2A), as has been shown for matrotrophically fed teredinid larvae (SHIPWAY, 2012).

Among deep sea mytiloids, apparently all Dacrydiinae have ST-2D; Atlantic species have been found at depths of 5280 m (ALLEN, 2008). Some species brood, but this is apparently not depth related (SALAS & GOFAS, 1997). Members of the Bathymodiolinae seep and vent faunas, such as *Bathymodiolus* KENK & B. R. WILSON, 1985, and *Gigantidas gladius* COSEL & MARSHALL, 2003, have typical ST-2A shells. Eggs are small, measuring between 40  $\mu\text{m}$  and 90  $\mu\text{m}$  (TYLER & YOUNG, 1999, table 5; LE PENNEC & BENINGER, 2000, table 1; ARELLANO & YOUNG, 2009), as in free-spawning planktotrophic mytilids. However, according to ARELLANO and YOUNG (2009), eggs of *Bathymodiolus childressi* GUSTAFSON & others, 1998, are negatively buoyant.

The genus *Adipicola* DAUTZENBERG, 1927, a dweller of organic falls in the deep sea, may be lecithotrophic (HORIKOSHI & TSUCHIDA, 1984; DELL, 1987). GÉNIO and others (2006) illustrated a specimen attributed to this genus, which has a ST-2D/ST-3C suggestive of brooding. Species of *Idas* JEFFREYS,



1876, have small eggs measuring up to 60  $\mu\text{m}$  (TYLER & others, 2009; OCKELMANN & DINESEN, 2011; GAUDRON, DEMOYENCOURT, & DUPERRON, 2012), and *Idas modiolaeformis* (STURANY, 1896) develops ST-2A (GAUDRON, DEMOYENCOURT, & DUPERRON, 2012), whereas DELL (1987) reports P-1 sizes of 133  $\mu\text{m}$  and 170  $\mu\text{m}$  for two *Idas* species, which would suggest somewhat larger eggs. DELL (1987) measurements of 500  $\mu\text{m}$  to 560  $\mu\text{m}$  for the prodissoconch of *Benthomodiolus lignicola* DELL, 1987, cannot be interpreted without additional information. The larvivorous species *Idas argenteus* JEFFREYS, 1876, is small, measuring, on average, 6 mm in shell length and does not brood (see OCKELMANN & DINESEN, 2011; for phylogenetic relationships, depth ranges, and habitats, see also GUSTAFSON & others, 1998; KYUNO & others, 2009; LORION & others, 2010).

LISIN, BARRY, and HARROLD (1993) and LISIN and others (1997) measured egg diameters of 180  $\mu\text{m}$  to 240  $\mu\text{m}$  in two species of large vesicomyids collected from cold seeps between 600 m and 900 m depth. Eggs and embryos were positive buoyant under laboratory conditions (LISIN, BARRY, & HARROLD, 1993). Uninduced spawning led to a high fertilization rate. Unfortunately, they did not provide information on the early shell. Small vesicomyids (4–15 mm) described by COSEL and SALAS (2001) have ST-2D (in 3 species) and ST-2C (in 1 species), measuring 160–240  $\mu\text{m}$ . It thus appears that vesicomyids are essentially lecithotrophic, although egg buoyancy experiments suggest planktonic development (LISIN, BARRY, & HARROLD, 1993; see also TYLER & YOUNG, 1999, table 4).

In summary, available data on egg sizes and shell types suggest conservatism of developmental modes within families and genera, with no strong relationship to water depth. This is indirectly supported by experimental studies showing that offspring of the deep-sea mussel *B. childressi* GUSTAFSON & others, 1998, from depths of ~540–2200 m, develop normally under surface pressures,

within ranges of 7° C to 15° C and in salinities of 35‰ and 45‰ (ARELLANO & YOUNG, 2011). Similarly, pressure experiments with shallow-water *Mytilus edulis* LINNAEUS, 1758, indicate that embryogenesis is normal up to 500 atm at temperatures of 10° C, 15° C, and 20° C (MESTRE, THATJE, & TYLER, 2009). In both cases, the main observed effect was a considerably slower development under the extreme abnormal conditions. These results are surprising given that pressure (sometimes synergistically with temperature) acts on the cellular (e.g., embryonic cleavage), molecular (enzymatic), and structural level (ordering structures and flexibility of lipid membranes, protein denaturation) (PRADILLON & GAILL, 2007). Early developmental processes and phases of bivalves thus appear rather pressure tolerant; depth-related factors do not obviously select against planktotrophy. Hence, presently available data do not support the classic Thorson-Rass rule (cf. JABLONSKI & LUTZ, 1983; PEARSE & LOCKHART, 2004; LAPTIKHOVSKY, 2006).

#### DEVELOPMENTAL MODES ALONG LATITUDES

On a global scale, the diversity of extant shelf bivalves declines from the tropics toward the poles, in correlation with higher speciation and relatively lower extinction rates in the tropics (CRAME, 2000; JABLONSKI, ROY, & VALENTINE, 2006; KRUG & others, 2009). With few exceptions, genera with the highest speciation rates are chief invaders of higher latitudes (KRUG, JABLONSKI, & VALENTINE, 2008, 2009). Comparable trends hold true for the Cenozoic (KRUG, JABLONSKI, & VALENTINE, 2009) and for the end-Jurassic Tithonian stage (CRAME, 2002). Three main factors are held responsible for this pattern: (1) high primary productivity and seasonal stability in the tropics versus a strong latitudinal gradient in seasonality of food availability toward the poles; (2) very low productivity in polar winters and, consequently, habitat extension of high-latitude species to exploit a wider range of food resources; and (3) resource occupation

by fewer species, which limits speciation and accommodation of invading species (VALENTINE & others, 2008; VALENTINE & JABLONSKI, 2010).

It has also been suggested that low seasonality and dependable, abundant trophic resources in the tropics favor larval planktotrophy (THORSON, 1950; JABLONSKI & LUTZ, 1983; LAPTIKHOVSKY, 2006). This would explain why developmental modes at higher latitudes tend to nonplanktotrophy or brooding. According to VALENTINE and JABLONSKI (2010), nonplanktotrophic species are increasingly diverse at higher latitudes because the decline in diversity with latitude is steeper for planktotrophs than for nonplanktotrophs.

In a macroevolutionary context, VALENTINE and JABLONSKI (2010) hypothesized that planktotrophy arose in Cambrian-Ordovician invertebrates in response to Cambrian phytoplankton diversification and the establishment of a spatial gradient in primary productivity (for an alternative or complementary view, see PETERSON, 2005). Changes in primary productivity, caused by global climatic turnovers, then became the principal factors leading to changes in the latitudinal diversity gradient. This pattern should be reflected by turnovers in planktotroph/nonplanktotroph ratios. This scenario appears plausible, even though it does not take brooding developmental modes into account. However, it should be tested on the basis of comparisons of early shell stages of congeneric species, not genera, before, during, and after major climatic changes. Whereas sufficient evidence for the Cambrian-Ordovician or any Paleozoic interval may not be available, Tertiary strata around the Eocene/Oligocene, Pliocene/Pleistocene, or Pleistocene/Holocene turnovers should contain sufficient well-preserved and easily accessible material for more definitive studies.

#### FUTURE RESEARCH

Most bivalve species are recognized solely on the basis of the morphology of their

adult shell, which is commonly convergent. Species determinations and inferences of phylogenetic relationship are obviously more reliable when based on additional, independent characters. The early shell can provide this additional information even for shells too immature to show characteristic adult features. Unfortunately, the early bivalve shell has been largely neglected in taxonomic descriptions and diagnoses, to a much larger degree than for gastropods, so that a sufficiently comprehensive comparative database does not yet exist. Studies of the early bivalve shell are also indispensable for reassessing homology hypotheses of hinge and ligament development, as well as for better understanding heterochronic processes involved in shell formation and perhaps also speciation. Tracing morphological developmental changes in the early shell might even provide a basis for elucidating underlying cellular or genetic controls and processes.

Previous sections have emphasized the importance of the early shell for inferences of developmental modes (p. 59 onward, herein), which are themselves key to hypotheses regarding the evolution of early life history. Although the early shell is not well suited for distinguishing levels of brooding, the presently defined early shell types should allow for more accurate differentiation between planktotrophic, ST-2A, and nonplanktotrophic developmental modes, ST-1 and ST-3, with intermediate morphologies, ST-2B and ST-2C, comprising a third, potentially phylogenetically informative group. These data are based on species-level observations, whereas biogeographic analyses are usually based on genera. However, unless we are able to evaluate developmental uniformity among species of the same genus, biogeographic patterns based on genera alone will not necessarily match the biogeographic distribution of life-history traits.

Some of the most intriguing unresolved issues for bivalve development relate to the assumed equivalence between egg size and egg energy. Assuming that buoyant eggs contain more lipids than demersal ones

(which appears likely), are the extra lipids found primarily in the yolk mass? If so, this would influence the energy content of the yolk (e.g., McALISTER & MORAN, 2012). Do similarly sized eggs of shallow- and deep-water species have comparable energy contents? Do buoyant eggs of deep-sea species expand during their upward drift? And do any of these questions have a bearing on prodissoconch-1 size or on our (overly?) simplified models of early life history?

Studies of early shell morphology cannot answer all of these questions, but they can clearly contribute to these and other questions relating to bivalve early life history, diversity, taxonomy, evolutionary processes, and interactions between bivalves and both local and global environmental dynamics.

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### ADDENDUM

This addendum provides references to recent publications that appeared during the final stages of preparation of the manuscript and editing and could therefore not be included in the analyses and discussion. Without thriving for completeness, the mentioned papers point at additional data on larval shell types, reproductive modes or alternative or complementary models of shell representation, image analysis, and on biogeographic diversity dynamics. It is worth pointing out that none of these papers was found to contradict conclusions drawn on the preceding pages.

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