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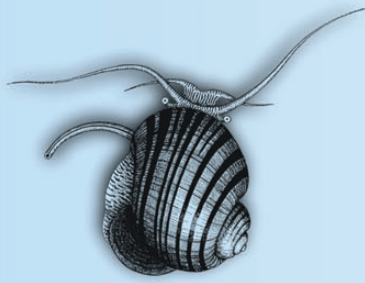
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MOLLUSCAN MARGINALIA: HIDDEN MORPHOLOGICAL DIVERSITY AT THE BIVALVE SHELL EDGE

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ABSTRACT

Molluscan shells exhibit a high and largely neglected diversity of serrations and crenulations at the growing margin. A survey of living and Cenozoic fossil bivalves indicates that serrations, in which the external ribs or interspaces between ribs extend radially beyond the general contour of the valve margin, may be symmetrical or asymmetrical. Projections whose adumbonal edge more nearly parallels the shell edge than the abumbonal edge occur on the posterior valve margins of many limids, cardiids and donacids, as well as in the arcid *Anadara* and a few concentrically ridged tellinids. In many cardiids, posterior serrations form as extensions of ribs, whereas ventral and anterior projections are extensions of rib interspaces. Asymmetrical serrations are almost always found on shell edges that are polished, indicating that the mantle extends slightly over the valve margin to the outside. I tentatively suggest that asymmetrical serrations enable the valves to close around siphons or other mantle extensions without injuring these soft tissues, so that the bivalve can maintain sensory contact with the environment even while the shell is shut. A preliminary comparison with brachiopods indicates that the diversity of conditions at the shell edge is much higher in bivalves. Together with the largely warm-water and marine distribution of marginal modifications in bivalves, these comparisons reflect the higher metabolic potentials of bivalves relative to brachiopods, and show that the shell edge is a rich source of evidence about function and mode of life in fossils.

INTRODUCTION

The accretionary skeleton, an anatomical external protective shell that grows at its expanding end and follows a basically spiral trajectory of growth, characterizes several animal clades including molluscs and brachiopods (Thompson, 1942; Vermeij, 1970). The shell margin, or generating curve, where growth in the spiral direction takes place, may lie in a plane or a more complex three-dimensional configuration (Raup, 1966). Its contour may be variously modified with crenulations, denticles, spines, notches, projections, thickenings and deviations from the prevailing growth direction. These may be produced continuously, periodically or only once at maturity, as reflected by sculptural elements on the outer and inner surfaces of the shell.

Despite their functional and taxonomic significance, these marginal modifications have remained little studied. Checa (2002) noted the important distinction between what he called strict contact guidance, in which the relatively mobile mantle margin of a bivalve creates and propagates deformations by aligning newly deposited skeletal material with structures already built, and reduced contact guidance, in which the more passive mantle has little information about previously formed deviations. Checa (2002) and Ubukata (2005) emphasized the formation of oblique sculptural elements rather than the nature of the deflections that give rise to these features. In gastropods,

many species have sharp lip edges, indicating a relatively inflexible mantle, whereas others have a polished outer lip either throughout life or at maturity, indicating reflection of the mantle over the lip's edge to the shell's exterior (Vermeij & Signor, 1992; Vermeij, 1998a; Kronenberg & Vermeij, 2002). Many predatory marine gastropods bear a node or spine projecting radially from the outer lip, formed at the end of either a spiral cord or an interspace between cords (Vignon, 1931; Vermeij, 1998b, 2001). Although much more work is needed to describe the range of marginal modifications in gastropods, my focus here is on bivalves.

The bivalve condition has evolved multiple times in molluscs, brachiopods, crustaceans and (as pods and silicles) in flowering plants (Thomas, 1988). In most cases, the valves are hinged together at one end, dorsal in the Bivalvia and posterior in rhynchonelliform brachiopods. When the shell is closed, part or all of the free edge of one valve meets the edge or inner side of the other valve. Plicated or internally crenulated valve margins align the valves during opening and closing, aided by the ligament, musculature and hinge dentition, and prevent the valves from shearing against each other when the shell is shut, a potentially effective adaptation against predators (Stanley, 1970, 1977; Reif, 1978; Thomas, 1978; Morton, 1980; Vermeij, 1983, 1993; Marsh, 1984; Coen, 1985; Villamil, Kauffman & Leanza, 1998; Kříž, 2007; Temkin & Pojeta, 2010). Moreover, tight articulation

of the closed valves aided by crenulations at the margins prevents the shell edges from splaying outward when the shell is subject to external compressive pressure by a forceful predator, enabling the shell as a whole to function as a pressure-resistant dome (Thomas, 2013). In some bivalves and brachiopods, the crests and troughs of marginal plications reflect the positions of sensory structures (Rudwick, 1964, 1965). High-amplitude zigzag margins, as in some oysters and brachiopods, keep the gap between the open valves narrow and, when combined with spines at the crests and troughs of the plicae, as in some rhynchonellacean brachiopods, prevent unwanted particles and predators from entering (Rudwick, 1964; Carter, 1968b; Westbroek, Yanagida & Isa, 1980). In the freshwater North American unionid genus *Epioblasma*, inwardly curving denticles at the posterior valve margins of the female shell function to hold fish as the valves are shut, so that the female can infect the trapped fish with glochidial larvae (Barnhart, Haag & Roston, 2008). Still other functions are suggested below.

The diversity of marginal modifications in bivalves has gone largely unnoticed. Beyond the frequent mention of crenulated inner valve margins and valve overlap in the taxonomic literature, other structures have been mentioned only in passing for limids (Allen, 2004), cardiids (Schneider, 1998a, 2002; Savazzi & Sälgeback, 2004), carditids (Beu, 2006) and verticordiids (Janssen, Peeters & van der Slik, 1984; Jung, 1996), among others. Checa (2002) and Checa & Jiménez-Jiménez (2003a, b) remarked on the properties of the mantle edge in bivalves with antimarginal and oblique ribs, but said little about the shell margin itself. Inferences about the formation of the periostracum, involving extension of the mantle margin beyond the valve edge, have been made for lucinids (Taylor & Glover, 1997; Taylor *et al.*, 2004), venerids (Taylor *et al.*, 1999; Glover & Taylor, 2010), Unionoidea (Checa, 2000), mytilids (Bottjer & Carter, 1980; Wright & Francis, 1984; Harper & Skelton, 1993; Harper, 1997), astartids (Salas *et al.*, 2012) and Anomalodesmata (Checa & Harper, 2010), but again the nature of the calcified valve edge received little scrutiny.

In order to clarify how the bivalve shell, and especially its free margins, forms and functions, it is important to describe variations on the theme of the shell edge and to assess the phylogenetic, ecological and geographical distributions of these variations, and to document how characters of the valve margin are related to features of sculpture, hinge dentition, locomotion and orientation. The result will, I hope, lead to a better appreciation of the shell as a functional, dynamic structure that is well integrated into the life of the animal constructing the shell.

My interest in this topic was rekindled first when I noticed by casual examination that some cardiid and donacid bivalves have two types of valve serration on different sectors of the valve edge, a condition that appears not to have been mentioned or investigated previously. A further impetus came from the realization that brachiopods and bivalved molluscs, two groups with dramatically contrasting evolutionary histories, differ in the diversity of their valve margins. Brachiopods were morphologically and taxonomically diverse in the Palaeozoic, but disappeared from most shallow-water marine habitats after the Jurassic, whereas bivalves have generally increased in taxonomic and functional diversity throughout the Phanerozoic and have dominated aquatic environments since the Early Triassic (Gould & Calloway, 1980; Fraiser & Bottjer, 2007; Song *et al.*, 2013). Understanding the valve-edge characteristics of bivalves and brachiopods will provide new evidence about how the ecological replacement proceeded.

The present paper offers a descriptive survey of marginal modifications in the shells of selected bivalves. In it I shall also suggest some defence-related hypotheses of the function of these modifications, make preliminary comparisons with brachiopods and discuss the relationship between marginal modification and

metabolic power in these two groups. The only modifications not discussed here are the formation of spines, which are common in productide brachiopods and many pteriomorphian bivalves, and flexible valve margins, well known in strophomenide brachiopods and pteriomorphian bivalves.

MATERIAL AND METHODS

I conducted a systematic survey of all fossil and living bivalves in my research collection, supplemented by observations on selected bivalves at the California Academy of Sciences (San Francisco) and the Florida Museum of Natural History (Gainesville). Most of the species studied range in age from the Early Miocene to the Recent, with all major clades represented. I have not attempted a comprehensive survey of all known taxa, because this can be done only by examination of well-preserved specimens and is beyond the scope of the present effort. Illustrations and descriptions in the literature do not suffice and are often unreliable for the level of detail required.

When referring to taxa, I use subgeneric names as full genera, even in cases where some recent authors have abandoned them, as in the arcid *Anadara s. l.* and the carditid *Carditamera s. l.* (Huber, 2010; Coan & Valentich Scott, 2012; González & Giribet, 2013). I have done so in order to highlight differences among closely related groups of species in the character of the valve margin.

Classifying marginalia

In order to facilitate description, I use the following definitions and conventions:

- (1) The free edge or margin of the shell (or valve) is the transition between the inner surface of the valve (facing the visceral mass) and the outer surface. It comprises sectors away from the points at the hinge where the valves articulate.
- (2) At each point along the free edge, growth occurs in a spiral direction. Spiral elements of sculpture (usually referred to as radial sculpture in the literature) are generated by successive positions of a given point along the free edge as the shell grows.
- (3) The commissure is the planar (or sometimes three-dimensional) curve of the free edge at a given stage of growth. Unless stated otherwise, I shall for convenience consider the commissure as lying in a plane.
- (4) The radial component of spiral growth lies in the plane of the commissure; the normal component of spiral growth is perpendicular to the plane of the commissure. The tangential component of spiral growth is parallel to the axis around which the valves rotate and within the plane of the commissure (Owen, 1953, 1958).
- (5) The angle of intersection is the angle between an external sculptural feature and the shell edge; if this angle is 0° , the sculptural element is concentric; if it is 90° , so that the element is perpendicular to the edge, the element is antimarginal (Waller, 1984, 2006a, b; Checa, 2002; Checa & Jiménez-Jiménez, 2003a, b; Ubukata, 2005).
- (6) The slope of growth is the ratio of growth in the normal direction relative to that in the radial direction. If this ratio is near zero, almost all growth is radial and therefore in the plane of the commissure; the valve is therefore flat. All growth is in the normal direction when the valve no longer expands in the radial direction, in which case growth is said to be vertical (Rudwick, 1959) and the valve is highly convex.
- (7) A crenulation is a repeated deflection of the inner free edge of the valve perpendicular to the inner valve surface. A zigzag margin (Rudwick, 1964; Carter, 1968b) occurs when crenulations are widely spaced and of high

amplitude (i.e. there is a large distance between crests and troughs), associated with serial folding (or plication) of the valve margin as a whole.

- (8) A serration is a repeated deflection of the free edge in the spiral direction of growth, produced as an extension of either an external rib or an external interspace between ribs. The high-amplitude equivalent is a lobe.
- (9) Marginal spines, scales or scutes are discontinuously produced extensions of external ribs projecting outward from the external shell surface.
- (10) Asymmetry of a crenulation or serration occurs when the lateral edges of the deflection have different slopes. In all cases, the adumbonal edge of the projection (the one closer to the umbo) is more nearly parallel to the contour of the margin as a whole than the abumbonal edge (the one facing away from the umbo). The effect is that the projection appears to be oriented in the ventral direction.
- (11) Interdigitation occurs when the serrations of one valve extend beyond the serrations of the other valve; the serrations therefore cross the plane of the commissure.
- (12) Valve overlap occurs when part or all of the free edge of one valve extends spirally beyond the commissure.
- (13) The free edge is said to be polished when the shell-secreting mantle margin is reflected over the calcified valve margin, so that the growing edge is covered by the mantle margin, and the edge is effectively formed by the inner shell layer. If this is not the case, the free edge is said to be sharp. Cases in which only the periostracum extends over the calcified shell margin are not considered polished.

These definitions are descriptive statements of the geometry of the valve margin, and thus imply nothing about the mechanism of formation or growth of the valve edge. As will be shown below, the various states described here are architecturally independent of each other. For example, crenulations can occur regardless whether the valve edge is serrated, and the pattern of serrations or lobes need not reflect the spiral expression of internal crenulations. Serial serrations and crenulations can occur on polished edges as well as on sharp ones; and asymmetry of these serial deflections likewise can, at least in principle, occur on polished as well as sharp valve edges. Patterns of occurrence and expression of the various marginal modifications are further elaborated in the discussion.

In many cases, extremely good preservation is required for the recognition of marginalia in fossil bivalves. For this reason, much of the descriptive account below is based on Recent species. Nevertheless, fossils can display these characteristics clearly, and palaeontologists are urged to examine fossil valve edges closely and systematically.

RESULTS

Arcoida

Four conditions of the valve margin occur in various combinations in members of the Arcoida: (1) a smooth edge; (2) an internally crenulated edge; (3) a serrated margin, rarely with asymmetrical projections posterodorsally and (4) overlapping valve margins, with the left valve posteroventrally and sometimes ventrally slightly overlapping the right valve. The marginal zone of the valves is almost always thickened by a concentric internal ridge, and in byssate species tends to be polished at and adjacent to the byssal gape. Although spiral ('radial') sculpture on the shell's exterior is nearly universal in the Arcoida, it is not always accompanied by a crenulated or serrated margin. For example, smooth valve edges occur in members of the *Arca imbricata* Bruguière, 1789 complex (including *A. avellana* Lamarck, 1819 from the Indo-West Pacific, *A. imbricata* from the western Atlantic

and *A. mutabilis* Sowerby, 1833 from the eastern Pacific); some species of *Barbatia s. l.* [e.g. *B. cancellaria* (Lamarck, 1819) from the Caribbean, *B. foliata* (Forsskål, 1775) from the western Pacific, the modioliform central Indo-West Pacific *B. obliquata* (Gray, 1837) and *B. virescens* (Reeve, 1844)] and the genera *Arcoptera* (Early Pleistocene of Florida), *Asperarca*, *Bathyarca*, *Bentarca* and *Trisidos* (see also Reinhart, 1935; Kilburn, 1983; Kamenov, 2007a, b; Francisco, Barros & Lima, 2012). The same condition occurs in some noetiids including *Arcopsis*, *Didimacar* and *Estellacar* (Vongpanich & Matsukuma, 2004), limopsids including *Nipponolimopsis* and several groups within *Limopsis* (Oliver, 1981; Amano & Lutaenko, 2004; Sasaki & Haga, 2007); and the cucullaeid *Cucullaea* (Morton, 1981).

The living eastern Pacific rock-boring arcid *Litharca lithodomus* (Sowerby, 1833) is unusual among arcids in having obsolete ventral crenulations and well-developed anterior and posterior ones. At the anterior end, each valve bears two rounded crenulations, whereas at the posterior end, at the terminus of the high external posteroventral keel, each valve bears one enlarged tooth. Although no other arcids I have seen bear this hitherto undescribed pattern of crenulation, at least two groups of arcids approach it. In *Acar plicata* (Dillwyn, 1817) from the Indo-West Pacific, the margin between the posterior end of the hinge line and the posteroventral angulation bears three strong crenulations, and the anterior margin has three weaker crenulations. Both sets of crenulations are more strongly expressed than the ventral crenulations, which extend along part or all of the ventral margin. The Caribbean *A. domingensis* (Lamarck, 1819) has a more uniform pattern of crenulation. A pattern of crenulation similar to that in *A. plicata* occurs in members of the *Arca zebra* (Swainson, 1833) complex, including the Caribbean *A. zebra*, the eastern Pacific *A. pacifica* (Sowerby, 1833), the West African *A. bouvieri* Fischer, 1874 and the Indo-West Pacific *A. navicularis* Lamarck, 1819 and *A. ventricosa* Lamarck, 1819. In these species and in *A. noae* Linnaeus, 1758 (the type species of *Arca*) from the Mediterranean, there are three anterior and three larger posterior crenulations, but the ventral margin (especially its posterior sector) has weak crenulations; the large byssal gape is smooth and polished. The pattern of crenulation in the *A. zebra* group sets that group of species, including *A. noae*, apart from the smooth-edged *A. imbricata* group, supporting previous suggestions that these two clades of *Arca* are phylogenetically distinct from each other (Oliver & Holmes, 2006). *Arca boucardi* Jousseume, 1894 is continuously crenulated along the ventral margin and has a much narrower hinge plate, and seems well removed from the *A. zebra* and *A. imbricata* groups.

Taxonomists have long recognized that overlap of the right valve by the left valve along the ventral margin is common, especially in the posterior sector. Examples occur in many anadardine taxa (*Anadara*, *Cunearca*, *Philippinarca*, *Scapharca* and *Sectiarca*) and in *Cucullaea*, all of which are burrowers. With the exception of the smooth-margined *Cucullaea* and of *Anadara* (see below), valve overlap is typically accompanied by a margin that is both crenulated and symmetrically serrated.

Serrated margins are widespread in the Arcidae, especially in the burrowing Anadardinae. Where present, the projections are formed as extensions of the ribs. Serration affects the whole free margin in strongly ribbed glycymeridids of the genera *Axinactis*, *Melaxinaea*, *Tucetona* and *Veletueta*. In the Early Pleistocene anadardine *Caloosarca crassicoستا* (Heilprin, 1886) from the Caloosahatchee Formation of Florida, exceptionally broad ribs form wide lobes on the posterior half of the ventral margin. The concave posterior margin of this species and of the living *C. notabilis* (Röding, 1798) from the Caribbean is not notably serrated. In most other arcoids with serrated margins, projections are either strongest on the posterior or posteroventral valve margin or restricted to those sectors. This is the condition in the eastern Pacific noetid *Noetia reversa* (Sowerby, 1833), the eastern Pacific

anadarine *Rasia formosa* (Sowerby, 1833) and the Indo-West Pacific *Anadara antiquata* (Linnaeus, 1758) (Fig. 1). Arcoid projections are generally symmetrical, but the posterior projections in *A. antiquata* show a slight asymmetry, with the adumbonal slopes more nearly parallel to the contour of the posterodorsal margin than the abumbonal slopes. This condition, together with the very slight overlap of the right valve by the left valve in the posteroventral sector (a characteristic overlooked by Reinhart, 1935; Olsson, 1961; and Noda, 1966, 1978, 1979, 1988, in their discussions of anadarine classification) distinguishes *A. antiquata* (Fig. 1) (type species of *Anadara*) from equivalve anadarine taxa such as *Caloosarca*, *Dallarca*, *Grandiarca*, *Hataiarca*, *Larkinia*, *Lunarca*, *Senilia* and *Tegillarca*.

The pointed asymmetrical projections of *A. antiquata* (Fig. 1) occupy the posterodorsal margin only and not the sector of valve overlap, where projections are symmetrical.

Pectinoidea

Members of the Pectinidae have valves with sharp, unpolished free edges without an internal concentric ridge. Smooth margins have evolved many times in the group, as in the genera *Amusium* and *Placopecten*, but in most pectinids the free edges are weakly to strongly plicated and also often finely crenulated according to the several orders of external radial sculpture present in most species. In many pectinids, the margin is radially lobed or serrated, with projections in all observed cases formed by extensions of interspaces between external radial or antimarginal elements. A weakly lobate valve margin occurs in *Pecten maximus* (Linnaeus, 1758) from Europe and in the northwestern Pacific *Swiftopecten swifli* (Bernardi, 1857), both of which are strongly plicated, but in

other plicated pectinids, the edge does not form repeated radial lobes. This latter condition is seen in the Indo-West Pacific genera *Annachlamys*, *Decatopecten* and *Mirapecten*; the North Pacific genera *Mizuhopecten* and *Patinopecten*, the tropical American genus *Nodipecten*, the Japanese genus *Notovola* and the Miocene and Pliocene eastern North American genus *Chesapecten*. Minute serration characterizes all examined species of the North Pacific and North Atlantic genus *Chlamys*, the tropical western Atlantic *Euvola ziczac* (Linnaeus, 1758) (left valve only, and not the overlapping right valve), the Indo-West Pacific *Glorigallium pallium* (Linnaeus, 1758) and the widespread Indo-West Pacific *Paschammites coruscans* (Hinds, 1845). A similar condition occurs in the European *Mimachlamys varia* (Linnaeus, 1758) and Indo-West Pacific *M. lentiginosus* (Reeve, 1853) and the New Zealand *Talochlamys gemmulata* (Reeve, 1853) and *T. zelandiae* (Gray, 1843). A more sharply dentate margin, in which the projections are again formed as extensions of interspaces between ribs, occurs in all species of the American genus *Argopecten* (Fig. 2) as well as in the tropical American Neogene genus *Interchlamys* (see also Waller, 2011).

Although pectinid projections are all formed in the same way, phylogenetic evidence (Waller, 1991, 2006a, b, 2011) indicates that they evolved independently within such clades as Chlamydinae and Pectininae (Pectinini, Decatopectinini and Aequipectinini). Such convergence is rampant in the Pectinidae with respect to external sculpture, development of internal ribs, cementation, swimming and gigantism (see also Salvi *et al.*, 2010; Alejandrino, Puslednik & Serb, 2011; Serb *et al.*, 2011).

In the related cemented family Spondylidae, variably long spines arising from external ribs extend beyond the valve margin. To my knowledge, no pectinid exemplifies this condition.

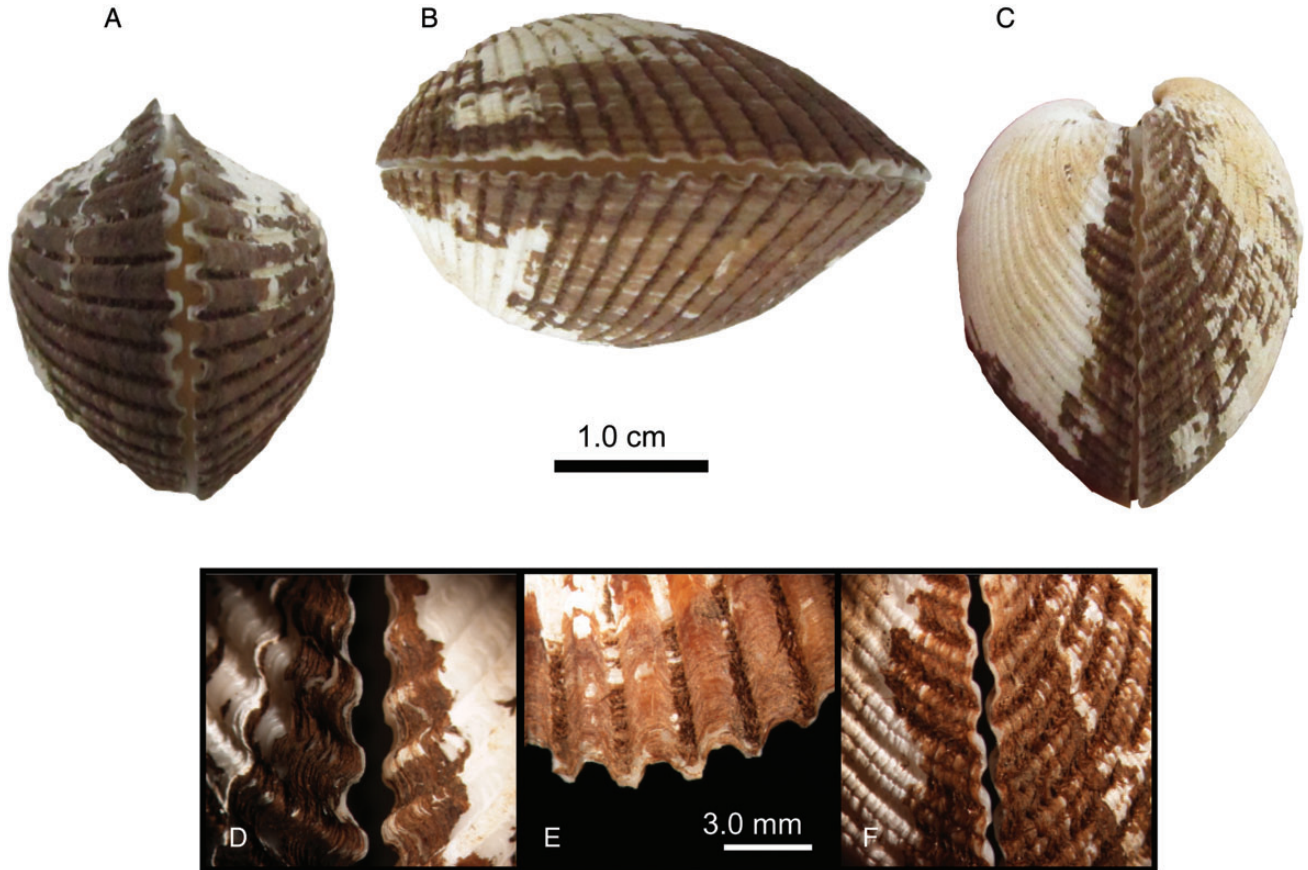


Figure 1. *Anadara antiquata* (Linnaeus, 1758) (Loloda Bay, Adui Island, Maluku, Indonesia; Vermeij collection). The posterodorsal margin shows asymmetrical serrations at the ends of ribs. **A.** View of posterior end, both valves. **B.** Ventral view, both valves. **C.** View of anterior end, both valves. **D.** Close-up of posterior margin, left valve. **E.** Close-up of posterior margin. **F.** Close-up of ventral margin.

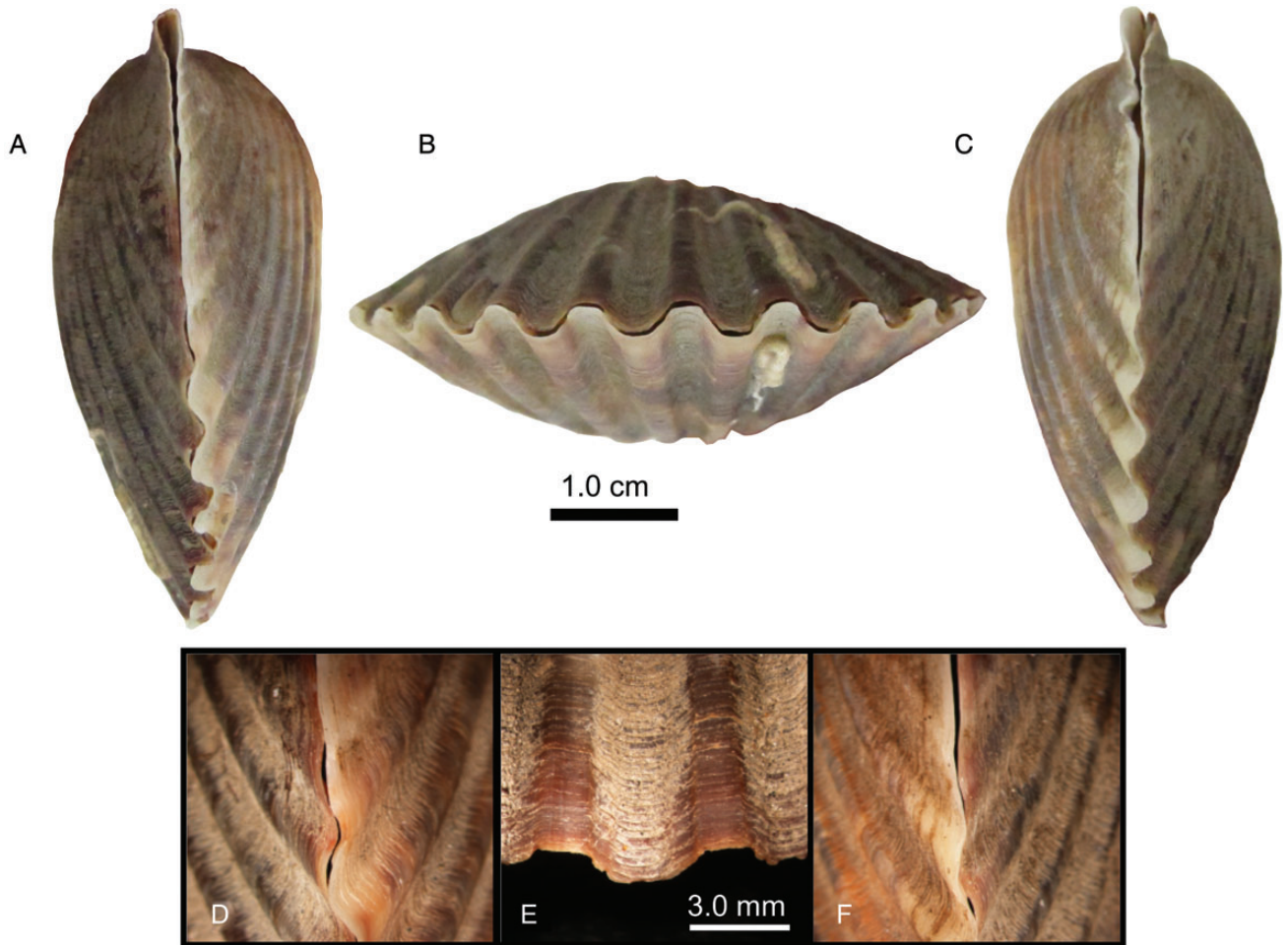


Figure 2. *Argopecten irradians* (Say, 1822) (Long Beach, NJ, USA; Vermeij collection). All serrations are symmetrical and formed at the ends of interspaces. **A.** View of posterior end, both valves. **B.** Ventral view, both valves. **C.** View of anterior end, both valves. **D.** Close-up of posterior margin, left valve. **E.** Close-up of posterior margin. **F.** Close-up of ventral margin.

Limidae

Although limids are convergent with pectinids in that many species have well-developed mantle eyes and are capable of swimming for short distances (Morton, 1979, 2000a, b, 2008), their shell margins differ strikingly from those of pectinids. In contrast to pectinids, in which the valve margins are sharp, limids tend to have polished margins. An internal concentric ridge characterizes the valve margins of *Ctenoides* and many species of *Limatula*, whereas in pectinids this ridge is absent.

Limids display several unusual conditions of the valve margins. In many species of *Limatula*, two or three crenulations on the ventral margin are enlarged relative to more lateral crenulations (Allen, 2004). In these species, these crenulations may partly replace hinge teeth, which are absent in *Limatula* (Allen, 2004). In species of *Ctenoides*, the valve margins are internally smooth (Mikkelsen & Bieler, 2003), but the anterior and posterior margins are minutely serrated. The projections, which appear to be formed as extensions or ribs, are slightly asymmetrical in such species as the Caribbean *C. scaber* (Born, 1778) and *C. mitis* (Lamarck, 1807) and the Indo-West Pacific *C. annulatus* (Lamarck, 1819), where the adumbonal slopes are more nearly parallel to the margin as a whole rather than the abumbonal slopes.

Carditidae

All members of the Carditidae have internally crenulated valve margins, which are separated from the rest of the interior valve

surface by a thickened concentric ridge. The ventral margin in byssate species of *Cardita* and *Byssomera* is distinctly polished. Valve overlap is unknown in the Carditidae and in the related families Astartidae and Crassatellidae.

In addition to crenulations, most carditids display serrated valve margins. In species with ovate to elongate shells, projections are strongest on the posterior margin and on the posterior sector of the ventral margin. This condition occurs in Neogene to Recent members of the genera *Cardita*, *Carditamera*, *Cardita* and *Glans*. In species with broadly ovate to circular shells, projections at the ends of ribs are distributed around the valve margin, although in the boreal genus *Cyclocardia* these projections (and the internal crenulations) are weakly developed. Projections are especially prominent in the Eocene to Early Oligocene North American genus *Rotundicardia*, but they are also distinct in the Eocene genera *Leuroactis*, *Pacificor*, *Venericardia* and *Venericor*, as well as in the living *Purpuricardia purpurata* (Deshayes, 1854) from New Zealand and in species of *Pleuromeris*.

Large specimens of the tropical eastern Pacific *Byssomera affinis* (Sowerby, 1833) and *B. bajaensis* (González & Giribet, 2013) and the Caribbean *B. gracilis* (Shuttleworth, 1856) are unusual among examined carditids in having rounded, lobate projections on the posterior margin and on the posterior half of the ventral margin formed not by ribs, as in other carditids, but by extensions of interspaces between ribs. Olsson (1961) did not draw attention to this condition when he compared *Carditamera s. s.* with his new subgenus *Byssomera*, and recent authors have

synonymized the two taxa (Coan & Valentich Scott, 2012; González & Giribet, 2013). My examination of *Carditamera floridana* (Conrad, 1846) from the southeastern United States, *C. radiata* (Sowerby, 1833) from the eastern Pacific and *C. apotegea* Gardner, 1926 from the Chipola Formation (Early Miocene) of Florida indicates that projections in these species are consistently formed as extensions on ribs. *Byssomera* and *Carditamera* appear to form a monophyletic group (González & Giribet, 2013), but separation of the two as distinct subclades would seem warranted on the basis of the condition of the valve margin.

Cardiidae

Cardiid valve margins are usually crenulated and serrated and do not exhibit either valve overlap or a thickened concentric ridge. Smooth or nearly smooth valve margins occur in the Jurassic to Miocene Lahilliinae (Schneider, 1992, 1995), brackish and freshwater members of the Lymnocardiinae (Vermeij & Dudley, 1985), the boreal clinocardiine genus *Serripes* and a few members of the Laevicardiinae.

The shell of all cardiiids is divided into two zones set off from each other by a radial ridge, angulation, keel or change in convexity extending from the umbo to the posteroventral margin. Anterior to this line, the central and anterior sectors of the valve edge form an evenly rounded planar curve. The posterior margin, lying behind the line of demarcation, is often straight and is polished in all cardiiids examined, indicating reflection of the mantle around the edge to the shell's exterior. The posterior edges of the apposing valves leave a gape of variable size according to species even when the shell is fully closed. Beyond these common features, cardiiids display considerable diversity in the morphology of the valve margins.

The simplest condition of serration in the Cardiidae is seen in species in which the projections around the free margin are all formed by extensions of ribs. This occurs in *Acanthocardia aculeata* (Linnaeus, 1758) and *A. tuberculata* (Linnaeus, 1758) from Europe, *Cardium costatum* (Linnaeus, 1758) and *C. indicum* Lamarck, 1819 from West Africa, *Chesacardium laqueatum* (Conrad, 1830) from the St Mary's Formation (Late Miocene) of Maryland, *Bucardium ringens* (Bruguière, 1789) from the Mediterranean and *Vepricardium setosum* (Redfield, 1846) from Java. All these taxa were assigned by Schneider (2002) to the Cardiinae. In *Chesacardium laqueatum*, the projections on the posterior margin are expressed as broad lobes, and the inner edge on that sector is only weakly crenulated. Rib-associated projections around the valve margin also occur in *Orthocardium subtorulosum* (d'Orbigny, 1850) from the Early and Middle Eocene of the Paris Basin, France, *Agnocardia acrocome* (Dall, 1900) from the Chipola Formation (Early Miocene) of Florida, *A. spinosifrons* Vokes, 1984 from the Pinecrest beds (Early Pliocene) of Florida and *Europicardium caparti* (Nicklès, 1955) from West Africa, all assigned by Schneider (2002) to the Orthocardiinae. The same condition occurs in all examined members of Fraginae (genera *Americardia*, *Apiocardia*, *Corculum*, *Ctenocardia*, *Fragum*, *Lunulicardia*, *Microfragum* and *Trigoniocardia*), the clinocardiine genus *Clinocardium* as represented by *C. nuttalli* (Conrad, 1837) from the North Pacific and the marine lymnocardiine genus *Cerastoderma*, represented by *C. edule* (Linnaeus, 1758) and *C. glaucum* (Bruguière, 1789), both from Europe (for classification and phylogeny, see Schneider, 1992, 1995, 1998a; Kirkendale, 2009). Projections are symmetrical and the whole free margin is polished in *Acanthocardia*, *Agnocardia* and *Fraginae*. In the other taxa considered, the posterior margin is polished, whereas the ventral margin is unpolished. The posterior projections are strongly asymmetrical and do not engage with those of the opposite valve in *Cardium indicum* and *Bucardium ringens*, which gape widely at both the anterior and posterior margins when the valves are shut. As noted by Savazzi (1985) and Savazzi & Sälgeback (2004), the projecting ribs in *C. costatum* are hollow at the valve margin.

The clade Tridacninae (Schneider, 1998b; Schneider & Ó Foighil, 1999; Keys & Healy, 2000) is characterized by strongly plicated valves. In all living species, broad interspaces between external plicae project as lobes beyond the general contour of the free valve margin. Scales or scutes that periodically arise on the plicae in *Chametrachea maxima* (Röding, 1798) and *C. squamosa* (Lamarck, 1819) project obliquely or perpendicularly rather than in the radial direction.

A more complex and striking pattern of marginal serration is seen in the genus *Dinocardium*, assigned by Schneider (2002) to the Cardiinae, and in the clade that Schneider (1992, 1995, 1998a) and Vidal (1999) referred to as the Trachycardiinae. In the latter clade, I have examined representatives of the genera *Acrosterigma*, *Dallocardia*, *Mexicardia*, *Trachycardium* and *Vasticardium*. All trachycardiines examined have polished, strongly serrated posterior margins, on which the projections are formed by extensions of the external ribs. These projections are consistently strongly asymmetrical, their adumbonal slopes lying subparallel to the posterior margin as a whole whereas their abumbonal slopes form nearly a right angle with the posterior margin (Fig. 3). The unpolished (sharp) ventral margin and the polished anterior margin are more weakly serrated, but here it is the interspaces between external ribs that project beyond the general contour of the margin and the serrations are symmetrical. In most species, the transition is formed by one or two larger, more strongly projecting ribs at the posteroventral corner. In extreme cases, as in the eastern Pacific *Mexicardia procera* (Sowerby, 1833) (Fig. 3), these enlarged projections are so long that they cross over from one valve to the other. In the southeastern North American *Dinocardium obliquum* (Spengler, 1799) and *D. robustum* (Lightfoot, 1786), the posterior serrations are broad, low, rounded, polished, symmetrical lobes formed by extensions of the ribs, whereas the weak serrations on the sharp ventral and polished anterior margins are more pointed, formed by extensions of the interspaces. It is surprising that the contrast between the posterior edge and the rest of the valve margin in these taxa has not been described previously, especially given the careful observations that have been made on characteristics of the ribs, interspaces, hinge and lunule (Stewart, 1930; Vokes, 1982, 1989; Vidal, 1999; Schneider, 2002; ter Poorten, 2009).

Donacidae

Members of the Donacidae have polished, usually crenulated and serrated valve margins delimited from the rest of the shell interior by a thickened concentric ridge. Smooth margins, however, occur in the Late Cretaceous genera *Adelphodonax* and *Alidodonax* (Saul, 1989), the West African freshwater *Galatea* (Vermeij & Dudley, 1985), the eastern Pacific and tropical Atlantic *Iphigenia* and the Indo-West Pacific *Hecuba*, *Latona* and *Plebiodonax*.

In several donacids with crenulated and serrated edges, some crenulations on the posteriormost sector of the ventral margin are slightly enlarged and more widely spaced than those elsewhere. This condition occurs in the West African *Donax rugosus* (Linnaeus, 1758) and in species of *Chion* including *C. caelatus* (Carpenter, 1857), *C. punctatostriatatus* (Hanley, 1843) and *C. ecuadorianus* (Olsson, 1961) from the eastern Pacific, and *C. denticulatus* (Linnaeus, 1758) from the Caribbean. No such enlargement occurs in the eastern Pacific *Chion obesus* (d'Orbigny, 1846), the Californian '*Donax*' *gouldii* Dall, 1921, the Indo-West Pacific *Deltachion semigranosus* (Dunker, 1877) and *D. spinosus* (Gmelin, 1791), the southeast North American *Paraserrula varibilis* (Say, 1822), and the genera *Paradonax* and *Carinadonax* in the eastern Pacific and *Cuneus* and *Serrula* in the northeast Atlantic.

Many tropical donacids are characterized by distinctly asymmetrical crenulations and serrations formed as extensions of radial ribs on the posterior margin just adumbonal to the

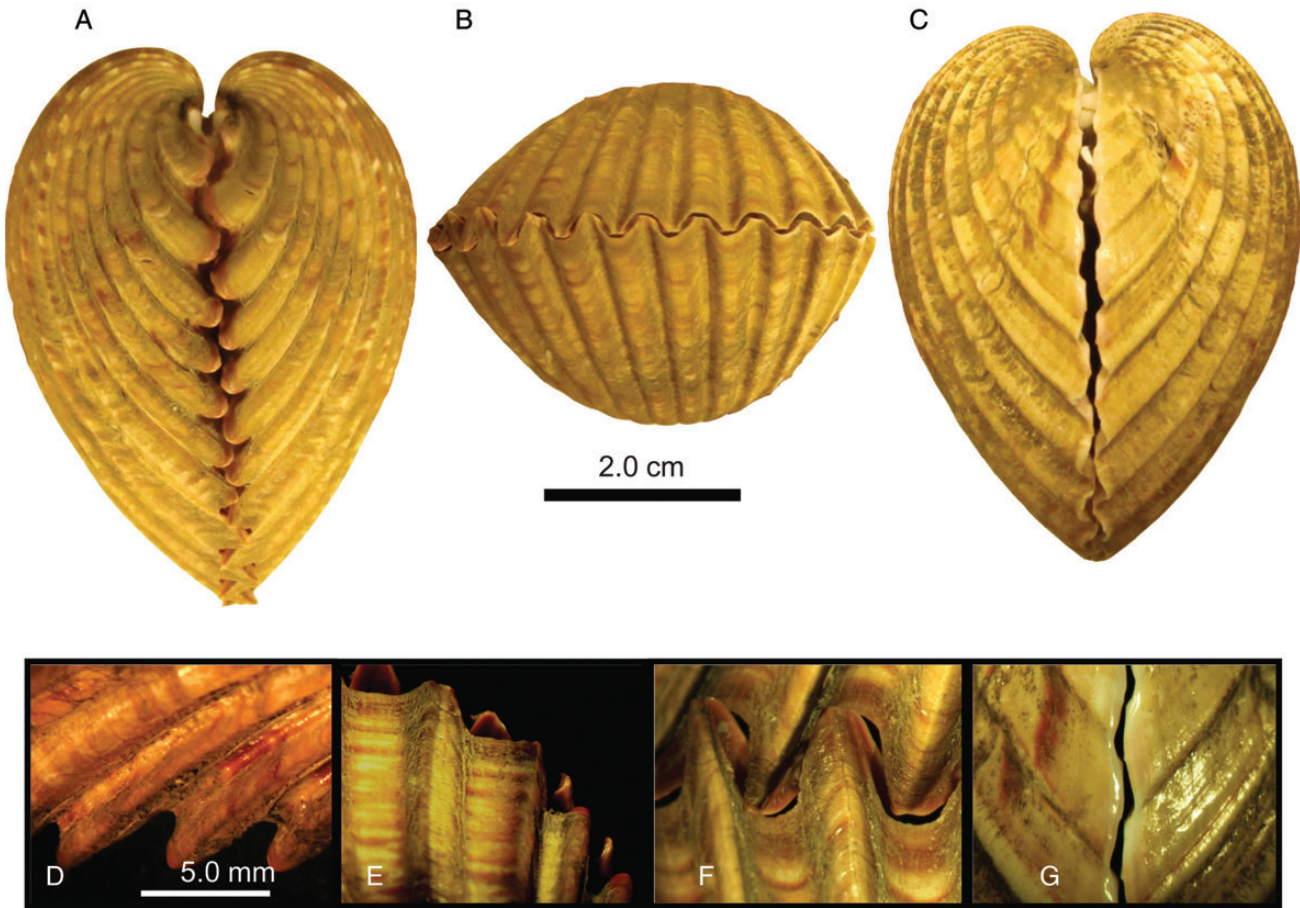


Figure 3. *Mexicardia procera* (Sowerby, 1833) (Playa Venado, Panama; Vermeij collection). Posterior serrations are polished, asymmetrical and formed at the ends of ribs. Serrations at the ventral margin are sharp and are at the ends of interspaces. Anterior serrations are polished and form at the ends of ribs. **A.** View of posterior margin, both valves. **B.** Ventral view, both valves. **C.** View of anterior margin, both valves. **D.** Close-up of posterior margin, left valve. **E.** Posteroventral corner with interdigitating ribs. **F.** Close-up of ventral margin. **G.** Close-up of anterior margin.

posteroventral angle. Such serrations, in which the adumbonal slope more nearly parallels the posterior margin than does the abumbonal slope, occur in *Donax rugosus*, '*D.*' *gouldii* and all examined species of *Chion* and *Deltachion*. In the sharply keeled eastern Pacific *Carinadonax carinatus* (Hanley, 1843) (Fig. 4) and to a lesser extent *C. transversus* (Sowerby, 1825), all serrations along the posterior margin are asymmetrical, whereas the ventral crenulations and serrations are symmetrical, as in the other taxa mentioned in this paragraph.

The right valve slightly overlaps the left valve near the posteroventral angle in eastern Pacific species of *Assimilidonax* (see also Coan, 1983; Coan & Valentich Scott, 2012). Two or three crenulations on the posterior margin and the posteroventral edge are notably enlarged relative to crenulations elsewhere, especially in *A. dentifer* (Hanley, 1845) and to a lesser extent in *A. assimilis* (Hanley, 1845) and *A. asper* (Hanley, 1845). All crenulations and serrations in these species are symmetrical. The large South African *Donax serra* Röding, 1798 lacks valve overlap but exhibits a similar but more subtle pattern of crenulations to that in *Assimilidonax*. Serrations on the posterior and posteroventral margins are symmetrical in other donacids examined, including the European *Serrula trunculus* (Linnaeus, 1758) and *Cuneus vittatus* (da Costa, 1778), the elongate smooth species *Paradonax californicus* (Conrad, 1837) and *P. gracilis* (Hanley, 1845), the Californian '*D.*' *gouldii*, and *Paraserrula variabilis* in the southeastern United States.

Tellinidae

Nearly all members of the Tellinidae have smooth, polished valve margins, but species in three genera of highly compressed species (*Phyllodina*, *Quadrans* and *Tellidora*) display short triangular spines projecting radially from the dorsal margin as extensions of concentric ribs. In the living Indo-West Pacific *Quadrans gargadia* (Linnaeus, 1758), six very short spines are situated behind the umbones of both valves on the dorsal margin. These projections do not engage; their adumbonal edges are nearly parallel to the dorsal margin, whereas their abumbonal slopes form a steep angle with that margin, making these six spines asymmetrical. Behind these six spines are three additional shorter symmetrical tubercles on the right valve and two on the left, those on the right valve forming small crenulations whereas those on the left valve do not extend to the inner edge of the dorsal margin. In *Tellidora cristata* (Récluz, 1842) from Florida and *T. burnetti* (Broderip & Sowerby, 1829) from the eastern Pacific, there are seven or eight slightly asymmetrical spinelets behind the umbo and three to five symmetrical spinelets in front of the umbo, again formed as extensions of concentric riblets; none of these projections crenulates the inner edge of the dorsal margin. Fine serrations formed as projections of external ribs occur in genera of the subfamily Strigillinae as well as in some specimens of the tellinines *Tellinella listeri* (Röding, 1798) from the Caribbean, *T. cumingii* (Hanley, 1845) in the eastern Pacific, *T. virgata* (Linnaeus, 1758), *Quidnipagus palatum*

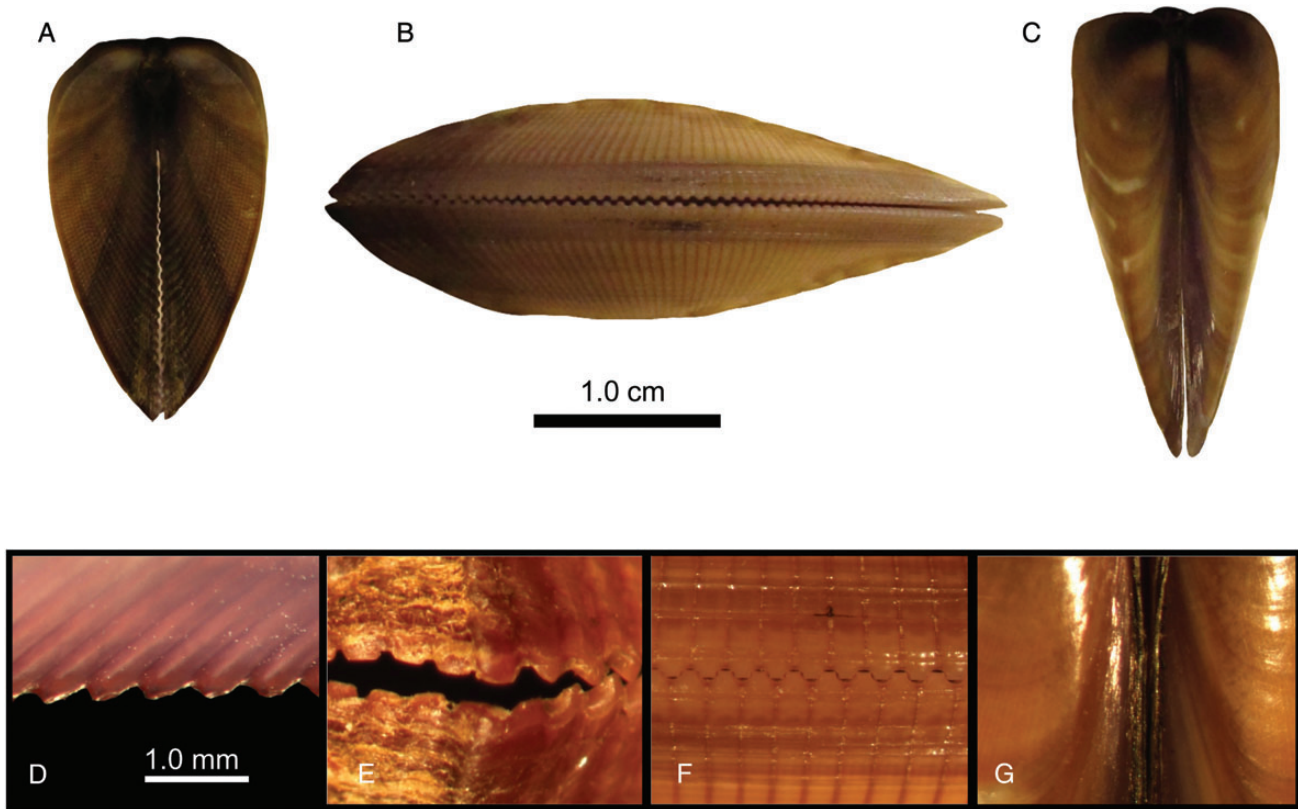


Figure 4. *Carinadonax carinatus* (Hanley, 1845) (Las Lajas, Panama; Vermeij collection). Posterior serrations and crenulations are fine, asymmetrical and formed at the ends of ribs; ventral serrations and crenulations are symmetrical. **A.** View of posterior end, both valves. **B.** Ventral view, both valves. **C.** View of anterior end, both valves. **D.** Close-up of posterior margin, left valve. **E.** Close-up of posterior margin. **F.** Close-up of ventral margin. **G.** Close-up of dorsal side.

Iredale, 1929, *Scutarcopagia scobinata* (Linnaeus, 1758) and species of *Scissula* in the Indo-West Pacific. Similar serrations are developed in the genus *Asaphis* in the related family Psammobiidae, especially on the posterior margin.

Veneridae

Most members of the Veneridae, a family of some 800 living species, have polished ventral valve margins and free edges that do not overlap. The only sharp-edged valves I have seen belong to species that Glover & Taylor (2010) identify as possessing long slender periostracal needles composed of aragonite, including members of the genera *Lioconcha* and *Gomphina*. As Glover & Taylor (2010) note, these taxa occupy a derived position within clade B, one of the two clades comprising Veneridae (Kappner & Bieler, 2006; Mikkelsen *et al.*, 2006). The only venerids with overlapping valves belong to the endolithic petricoline genus *Claudiconcha* (Morton, 1978; Savazzi, 2005).

Marginal ornamentation is widespread in the Veneridae and appears to have evolved from smooth-edged forms multiple times. Crenulation characterizes the clades Chioninae, Circinae, Sunettinae and Venerinae, although with rare exceptions (*Glycodonta* in Chioninae) it does not affect the posterior valve margin. Where serration occurs, it tends to be very fine, as in the chionines *Chionopsis*, *Glycodonta*, *Austrovenus* and *Leukoma*, as well as in the venerine *Periglypta* and the circine *Gafrarium*. Projections of the ventral margin are most pronounced in species of *Glycodonta* and *Periglypta* with pronounced radial ribs. Venerid clades with consistently smooth margins include Callistinae, Dosiniinae, Lioconchinae, Pitarinae, Samarangiinae and Tapetinae. Apparently all members of clade B have smooth

margins, as do members of the related families Arcticidae and Glauconomidae.

Beyond this relative uniformity, venerids display two minor and rare variations of the valve margin. In the living New Zealand chionine *Austrovenus stutchburyi* (Wood, 1828), the crenulations immediately adumbonal of the posteroventral angulation are slightly enlarged relative to the crenulations on the ventral margin. I have not seen this condition in any other venerid. In the Pliocene eastern North American chionine *Mercenaria tridacnoides* (Lamarck, 1818), three or four low, broad, rounded radial waves cause the commissure to develop a shallowly zigzag configuration. The external troughs end in broad projecting lobes at the ventral margin.

Finally, the smooth-edged pitarine tropical American genus *Hysteroconcha* periodically produces two rows of mantle-enclosed spines on external ridges well beyond the posterior margin. These spines likely have a defensive function (Carter, 1967).

DISCUSSION

Bivalves exhibit a surprising diversity of conditions of the free shell margin. Most of this diversity has received little attention, and several features have not been noticed previously at all. I discuss these conditions in turn below, suggest some functional explanations, and compare the diversity of valve marginal characteristics in bivalves with those in brachiopods.

Asymmetrical serration

The previously overlooked condition of asymmetrical serrations and crenulations on part of the free valve margin has evolved in

widely scattered parts of the bivalve phylogenetic tree. It has evolved in Pteriomorpha (Arcidae and Limidae) and Heteroconcha (Cardiidae, Donacidae and Tellinidae), altogether a minimum of five times independently at the family level.

All cases of asymmetrical serration are associated with projecting ribs rather than with projecting interspaces. In most cases, these ribs are spiral ('radial'), but in tellinids they are concentric (as in *Phyllodina*, *Quadrans* and *Tellidora*). The asymmetry is generally concentrated on the posterior and posterodorsal sectors of the valve margin, but in limids of the genus *Ctenoides* it also affects the anterior edge.

The sectors of the valve margin where asymmetrical serration is expressed are generally more exposed to disturbance from the outside than are other sectors. Most bivalves with asymmetrical marginal projections are shallowly buried in sediment, with the posterior or posterodorsal parts closest to the sediment surface. Limids are active epifaunal clams that can attach by a byssus as well as swim. Species with asymmetrical serration are known mainly from shallow tropical or subtropical marine waters. With the exception of the arcid *Anadara*, which is a slow burrower, bivalves with asymmetrical marginal serration are highly active animals capable of swimming, leaping or rapid burrowing. Adduction of the valves tends to be rapid. It must be noted, however, that active bivalves using jet propulsion to swim or burrow lack asymmetrical serration, as in pectinids, solenids, cultellids and solecurtids.

Again with the exception of *Anadara*, shell edges with asymmetrical serrations are polished, indicating a mobile mantle margin capable of extending over the valve margins to the shell exterior. Because the projections from one valve engage with those of the other when the shell is closed, the full effect of the sharpness of the asymmetrical projections is evident only when the valves are even slightly parted. The asymmetry of each projection is consistent: the adumbonal edge is more nearly parallel to the overall contour of the valve margin than the abumbonal edge.

These facts lead me to the hypothesis that asymmetrical serration and crenulation along polished valve margins enable a bivalve to shut the shell securely while maintaining sensory contact with the outside with organs that remain uninjured even as the valves are closed. Few human tools that cut, saw or grip—pliers, knives, saws, scissors and tweezers—have asymmetrical ridges or teeth along their edges. However, Jessica Bean (personal communication, February 2013) informs me that some surgical scissors that are designed to hold but not to break delicate tissues do have asymmetrical teeth along their apposing edges. Rather than shearing the tissue between closing blades, as would occur when serrated pliers or scissors are applied to delicate elastic fibrous materials, surgical scissors with asymmetrical serrations grip the target material without causing damage.

Among animals, apposing asymmetrical serrated structures occur in the bills of certain nectar-robbing hummingbirds (Ornelas, 1994), mergansers (*Mergus* spp.) and toucans (Rhamphastidae). In hummingbirds and mergansers, the serrations point backward towards the base of the bill (Ornelas, 1994; Van Grouw, 2013; personal observations on *Mergus merganser* Linnaeus, 1758 and *M. serrator* Linnaeus, 1758, at the California Academy of Sciences), whereas in toucans they point forward (Van Grouw, 2013). The backward orientation presumably helps the birds tear the base of flowers or to hold struggling fish. The function of the forward-pointing serrations in toucans is unclear.

In the case of active bivalves, the siphons or posterior edge of the mantle, which can wrap around the serrated polished valve margin, could be partially withdrawn as the valves close, but not so far as to prevent the sense organs located on them from detecting potential danger. In their partially retracted position between the shut valves, the sensory tissues could be held in place but not injured as the two valves engage. Detection of danger, such as the presence of a predator, could then elicit an

effective escape response. These circumstances should apply to highly active bivalves living in warm, shallow waters where the potential to move rapidly is great. Bivalves that burrow slowly, or that are permanently attached, hermetically sealed inside the shell, or living in environments where risks are lower (such as in cold water) should not experience selection in favour of asymmetrical serration.

Other marginal modifications

Symmetrical serrations and crenulations, polished valve margins, and valve overlap at the free margin are phylogenetically, ecologically and geographically more widespread than asymmetrical serrations. Symmetrical serrations, for example, occur in slow burrowers (arcids, lucinids, carditids, venerids, verticordiids and some periplomatids), fast burrowers (donacids and cardiids) and active epifaunal bivalves (pectinids and limids). A crenulated or plicated margin without radial projections is very common among species attached to hard substrata (mytilids, arcids, pectinoideans, ostreodeans and chamids) and slow to moderate burrowers (nuculids, arcids, lucinids, kelliellids, astartids, crassatellids, venerids and some corbulids). Polished valve edges occur very widely, especially in active burrowers. They are notably absent in ostreodeans and pterioideans as well as in attached and active pectinoideans. Valve overlap evolved many times in Pectinoidea, Ostreoidea, Arcoidea, Myoidea (including Corbulidae) and Anomalodesmata (Nicol, 1958; Vermeij, 1983), as well as in the donacid *Assimilidonax* (see above). Although the frequencies of all these modifications in local bivalve assemblages are higher in warm shallow seas than in cold marine waters (Vermeij, 1993), examples of all of them can be found at all depths in the ocean throughout the world. As noted by Carter (1968a) and Vermeij & Dudley (1985), freshwater bivalves show a very low incidence of crenulated margins and valve overlap, with serration apparently being wholly unknown among freshwater bivalves. The only cases of valve overlap in fresh water occur in members of the myoidean families Corbulidae and Freissenidae (see also Anderson, Hartman & Wesselingh, 2006; Anderson, Wesselingh & Hartman, 2010).

The only condition that is at all common in freshwater bivalves is a plicated margin, in which the plicae are oblique (Watters, 1994). The plicate portion of the shell typically protrudes above the sediment surface. Strongly plicate margins in marine bivalves are almost all restricted to epifaunal and shallowly infaunal species, including members of the Pectinidae, Plicatulidae, Anomiidae (*Placunanomia*), Ostreoidea, Pinnidae, Mytilidae (the Miocene North Pacific *Plicatomytilus*), Carditidae, Donacidae (*Tridonax*), Chamidae (*Arcinella*), post-Triassic Trigonioidea and Mesozoic Inoceramidae (Yoshida, 1998; Savazzi & Sälgeback, 2004; Huber, 2010). Whether the folded margin itself functions in these bivalves is unclear, but the external sculptural elements generated by it serve to stiffen the valves against bending (Reif, 1978; Pennington & Currey, 1984; Alexander, 1990a, b; Savazzi & Sälgeback, 2004). Similar stiffening, but then without marginal deviations, occurs in concentrically corrugated, thin-shelled, slow-burrowing mactrids such as *Harvella*, *Macrinula*, *Raeta* and *Raetellops* (see also Morton, 2010; Signorelli, 2013) as well as in some thraciids, inoceramids and the Middle Permian genus *Kolymia* (Checa & Crampton, 2002; Biakov, 2012). Similarly, the very fine crenulations on the inner valve margin of some bivalves may be an incidental by-product of the formation of external oblique or radial ribs, which function in burrowing or in preventing sediment scour around the shell (Stanley, 1969, 1970, 1975, 1981; Savazzi, 1982; Watters, 1993, 1994; Savazzi & Sälgeback, 2004).

In cases where crenulations do appear to have direct functions, they are to one degree or another associated with passive defence against predators that attempt to break the shell, enter the shell

between gaping valves, or drill a hole at the valve margin (Vermeij, 1983). As noted in the introduction, crenulations either maintain valve alignment, especially when shearing forces are applied when the valves are shut, or resist valve deformation in the radial direction when compressive forces are applied. In the majority of bivalves, the most vulnerable sectors of the free valve margin are the posterodorsal, posterior and posteroventral edges. These are also the sectors in which enlarged crenulations and serrations are situated. In addition to the cases discussed earlier under Arcidae, Limidae, Donacidae, Veneridae and Cardiidae, two others may be briefly mentioned here. In the Pliocene to Recent Floridian lucinid *Lucina pennsylvanica* (Linnaeus, 1758), a prominent external groove extending from the umbo to the posteroventral margin is expressed on the inner valve edge of both valves as a distinct bulge, which likely complements the fine crenulations along the rest of the free edge to align the valves and to resist compression. In the Permian pterioidean genus *Cassiavellia*, there are two enlarged condyles, one posterior and the other anterior, which together function in valve articulation (Tëmkin & Pojeta, 2010).

Marginal serrations or lobes may be formed by extensions of either ribs or interspaces between ribs. In some cardiids, these two conditions co-occur in the same shell. Projections as extensions of ribs are the rule in serrated donacids, venerids, arcids and most carditids, whereas projections at the ends of interspaces characterize pectinids, tridacninae cardiids, the carditid *Byssomera* and the venerid *Mercenaria tridacnoides*. Whether there are functional differences between the two types of projections is unknown.

Valve overlap also tends to be concentrated along the posteroventral sector. If the margin of the larger valves sustains damage, the seal between the closed valves is not necessarily compromised. It is notable that the strong crenulations on the posteroventral sector of the larger valve in anadarine arcoids are directly exposed to the external environment when the valves are closed, and therefore do not engage with the crenulations of the smaller valve. They therefore cannot function to prevent compression or to improve articulation along that sector of the shell margin.

It is interesting to note that, with few exceptions, the marginal ornamentation in bivalves forms continuously during part or all of postlarval ontogeny. An exception is the formation of an internal marginal hook at the shell's posterior in females of the North American unionid *Epioblasma* (Barnhart *et al.*, 2008). In this respect bivalves differ strikingly from numerous caenogastropods and heterobranch gastropods, in which denticles and even spiral lirae on the inner shell surface form periodically during growth or only at maturity (Vermeij & Signor, 1992). In contrast to bivalves, in which the commissure of fully grown adults differs little from that of younger individuals, gastropods often exhibit striking apertural modifications in the adult stage or periodically during spiral growth (Vermeij & Signor, 1992).

Comparisons with brachiopods

Despite their great variety of shell forms, especially during the Palaeozoic, brachiopods are much more uniform in the condition of their valve margins than are bivalves. To my knowledge, no brachiopods have asymmetrical serrations. None has lobes or serrations that form as extensions of rib interspaces and none shows differentiation between sectors of the free valve margins. All serrations in brachiopods appear to be symmetrical and all form at the growing ends of plicae or costae (see also Rudwick, 1965; Westbroek *et al.*, 1980). Differentiation of the valve margin is widespread in the Bivalvia, in which the posterior sector has a slope, sculpture and marginal characteristics distinct from those of the median to anterior sector of the free valve edge. This differentiation hints at separate genetic controls on these two sectors. Matsukuma (1996) had already noted that bivalves

showing hinge transposition, where the dentition typical of the right valve instead occurs in the left and vice versa, have two domains of dentition that vary independently. Transposition typically affects only the posterior or anterior sectors, but not both. The only bivalves in which such a bipartite division is not evident from shell morphology are some pteriomorphians, including Glycymerididae, Limopsidae, Pectinoidea, Pterioidea and Ostreoidea. With few exceptions (Fürsch & Palmer, 1984), brachiopod valves are bilaterally symmetrical about the antero-posterior midline, and therefore do not exhibit the sectorial differentiation around the free valve edge seen in many bivalves.

Two other conditions are common in bivalves but very rare in brachiopods. Polished edges are phylogenetically widespread in the Bivalvia, but in brachiopods valve margins tend to be sharp. The only exceptions are some Late Palaeozoic productides in which the lid-like upper valve appears to be encased in mantle tissue in some cases (Rudwick, 1961; Cowen, 1970). These productides are also exceptional among brachiopods in exhibiting valve overlap along edges away from the hinge.

Some of this lack of diversity in brachiopod shell margins might be blamed on the poor representation of the infaunal habit among brachiopods. The only indisputably infaunal brachiopods are linguliforms, but their shells are simple, smooth-edged structures. In any case, as shown above, epifaunal bivalves show considerable variation in the condition of the valve margins. Comparisons between brachiopods and bivalves should be made among epifaunal taxa (Vermeij, 1987) and these reaffirm the lower marginal diversity among brachiopods.

The most important factor contributing to the greater variety of valve margins in bivalves compared with brachiopods may be exposure to predators. Most of the modifications highlighted in this paper occur in bivalves living in environments where a high diversity of predators, many of them using active means to search for and subdue their victims, has evolved. Brachiopods, in contrast, are generally restricted to deeper, colder, more cryptic environments than bivalves, and are exposed to smaller, slower predators. Although Palaeozoic and Early Mesozoic brachiopods occupied a much greater range of habitats, including reefs and other shallow tropical habitats, predation was on the whole less intense than during the bivalve-dominated Late Mesozoic and Cenozoic eras. Most of the antipredatory traits exhibited by brachiopods—plicae, zigzag margins, spines, cementation and flexible margins (Alexander, 1990a, b; Leighton, 2001)—are passive defences. Traits associated with mobility and with aggressive or active defence are much less obvious in brachiopods than in many bivalve clades.

Finally, living bivalves show a substantially greater range of metabolic rates than brachiopods (Peck, 1992) and are therefore more likely to exploit defences and modes of life that are associated with high levels of activity. Whether this difference also applied during the heyday of the brachiopods remains an open question. Indeed, it is far from certain that Palaeozoic bivalves exhibited the high diversity of marginal modifications seen in their post-Triassic counterparts. Exploration of these issues will require the development of reliable proxies of metabolic activity in fossils as well as the descriptive evaluation of shell edges in Palaeozoic and Mesozoic bivalves and brachiopods.

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