



## Phylogeny and escalation in *Mellopegma* and other Cambrian molluscs

Michael J. Vendrasco, Artem V. Kouchinsky, Susannah M. Porter, and Christine Z. Fernandez

### ABSTRACT

*Mellopegma* Runnegar and Jell is a widespread Cambrian stenothecid helcionelid mollusc that may represent the ancestral state of rostroconchs. New fossils provide details about the morphology and evolution of this genus.

Many specimens show healed wounds, indicating *Mellopegma* experienced frequent predation. Common scars near the sub-apical aperture indicate this area was a favoured target. Predation may have led to the formation of the strengthening zygon in this region of the possible descendent *Eurekapegma* MacKinnon. *Mellopegma* exhibits many anti-predator traits, and preliminary analyses herein show: 1) *Mellopegma* became better defended through time via aperture narrowing; and 2) stenothecids show an increase in proportion of damaged shells from early to middle Cambrian deposits. This evidence is consistent with an early arms race between predators and molluscan prey.

Specimens from Siberia reveal that calcitic semi-nacre has a deeper history in the Mollusca than previously thought, consistent with the hypothesis that this shell microstructure occurs in both molluscs and brachiopods due to homology in the organic framework for shell formation. The shell of *Mellopegma* contained pores and the commonality of this trait among early molluscs suggests a porous shell may be primitive in Mollusca. The protoconch/teleoconch boundary is distinct in many specimens and indicates the fossils are of adult shells, and *Mellopegma* was lecithotrophic. One specimen of *Mellopegma* preserves the periostracum.

*Mellopegma schizocheras* sp. nov. is described from the middle Cambrian of Australia. *Anabarella simesi* MacKinnon is transferred to *Mellopegma*. *Ribeiria junior* Runnegar is removed from Rostroconchia and transferred to the new genus *Acanthotheca*.

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## INTRODUCTION

Molluscs occur in many of the earliest shelly assemblages and clearly began to diversify in the early Cambrian. Most of the earliest shelled molluscs were univalves with slight coiling (referred to as helcionellids) but some had shells with greater coiling (possible gastropods or their ancestors), a few others were bivalves (Pojeta 2000), and chitons might also have been present (Vendrasco et al. 2009). There is much gradation in form among these early molluscs, and hence different possible transitional sequences in the fossil record have been identified from helcionellids to rostroconchs, bivalves, scaphopods, gastropods, and cephalopods (e.g., Runnegar and Pojeta 1974, Pojeta and Runnegar 1976, Kouchinsky 1999). These evolutionary scenarios and the relationships among the earliest molluscs remain controversial, however, because there are so few characters that are well known from their fossil shells. Further complicating the issue is that at least some helcionellids appear to represent the larval shell of an adult form that looks somewhat different (Martí Mus et al. 2008).

Pioneering work by Runnegar (1985) revealed that phosphatic shell moulds and replacements of Cambrian molluscs preserve details of their shell microstructure in sub-micrometer detail. Runnegar showed that secondary calcium phosphate coatings on the inner shell surface – probably precipitated as a result of bacterial decay shortly after the death of the animal (Lucas and Prévôt 1991) – could preserve imprints of shell microstructures in both inner and outer shell layers. Runnegar (1985) documented that some of the more common varieties of shell microstructure in modern molluscs (e.g., crossed lamellar, prismatic, foliated calcite) also occurred in Cambrian forms. Shell microstructure is rarely preserved in early Palaeozoic fossils, and so Runnegar's work revealed a new suite of characters that could be used to better understand the degree of diversification, phylogeny, and shell strength of the early molluscs. More recent observations (Kouchinsky 1999, Vendrasco et al. 2010) indicate that shell microstructures have a strong phylogenetic signal and hence can help in assess-

ing hypotheses of relationships and transitions among early molluscs.

The rapid diversification of animals beginning around 542 million years ago was one of the most significant events in the history of life. This event, known as the "Cambrian Explosion," is characterized by the independent appearance and rapid diversification of shells in many animal lineages (Bengtson and Conway Morris 1992). Although there have been significant advances over the past few decades in our understanding of this interval, we are far from knowing the causes of the event. One of the more prominent hypotheses about the Cambrian explosion is that it was caused by the onset of predation, which likely drove adaptation in various lineages toward diverse defensive solutions. Information about early predators and the response of their prey is rather limited, but a number of observations suggest predation was a strong selective pressure in the Cambrian: (1) the earliest signs of predation occur at the base of the Cambrian or just before (Bengtson and Zhao 1992); (2) many different types of fossil evidence of predation have been recovered from Cambrian rocks, including predatory appendages on fossil arthropods (Whittington and Briggs 1985), drill holes (Conway Morris and Bengtson 1994), bite marks (Conway Morris 1998), ingested prey preserved in the digestive tract of predators (Whittington 1985), and healed shell scars (Skovsted et al. 2007); and (3) shells, thought by many to be primarily a tool of defense (Vermeij 1987), appeared in many different animal lineages during the Cambrian explosion (Bengtson and Conway Morris 1992) and were made of diverse components and with different microstructures (Bengtson and Conway Morris 1992), and so likely evolved independently in many clades. Nevertheless, in spite of this preliminary support, the hypothesis that predation was a major driving force of the Cambrian explosion is still disputed.

*Mellopegma* Runnegar and Jell, 1976 is a stenotheacid found in Cambrian deposits worldwide (Table 1). Stenotheacids are helcionellid molluscs with significant lateral compression (Runnegar and Jell 1980). They also have a curved ventral margin,

**TABLE 1.** List of species that have been assigned to *Mellopegma*, including those considered here to belong to other genera.

| Species assigned to <i>Mellopegma</i>                       | Age and location                            | Notes   |
|---|---|---|
| <i>M. georginense</i> Runnegar and Jell, 1976               | middle Cambrian, Australia                  | type species; from Gowers Formation                                     |
|   | late early Cambrian, U.S.A.                 | described by Landing et al. 2002  |
| <i>M. simesi</i> (MacKinnon, 1985) comb. nov.               | middle Cambrian, Australia, and New Zealand | assigned here; originally <i>Anabarella</i>                             |
| <i>M. nana</i> Zhou and Xiao, 1984                          | early Cambrian, China                       | transferred to <i>Figurina</i> by Parkhaev in Gravestock et al. 2001    |
| <i>M. indecorum</i> (Missarzhevsky in Rozanov et al., 1969) | early Cambrian, Russia                      | previously in <i>Anabarella</i>   |
| <i>M. uslonicum</i> Parkhaev, 2004                          | early Cambrian, Russia                      |   |
| <i>M. schizocheras</i> sp. nov.                             | middle Cambrian, Australia                  | co-occurs with <i>M. georginense</i> and <i>M. simesi</i>               |
| <i>M. rostratum</i> Zhou and Xiao, 1984                     | early Cambrian, China                       | transferred to <i>Mackinnonia</i> by Parkhaev in Gravestock et al. 2001 |

as do bivalves and rostroconchs, the latter an extinct class of molluscs with a univalved larval shell and bivalved but inflexible adult shell (Pojeta 1987). In part because stenothechids have a shell form intermediate between typical helcionellids and the two bivalved mollusc classes, they – in particular *Mellopegma* – were considered possible ancestors of bivalves and/or rostroconchs (Runnegar and Jell 1976; Runnegar 1978, 1996; Pojeta 1978).

Our goal was to utilize the large number of specimens of *Mellopegma* to refine the taxonomy of this genus and ascertain its detailed morphology. Most of our specimens are from the middle Cambrian Gowers Formation, Georgina Basin, Australia, including the type species very near the type locality (Figure 1; Vendrasco et al. 2010, figure 1b). We discuss the implications of this new information for understanding the functional morphology, diversity, and evolution of this genus, as well as the evolution of molluscan shell pores and microstructures, homology with shells of brachiopods, nature of escalation between molluscs and their predators during the Cambrian, and the origin of the molluscan classes Rostroconchia and Bivalvia.

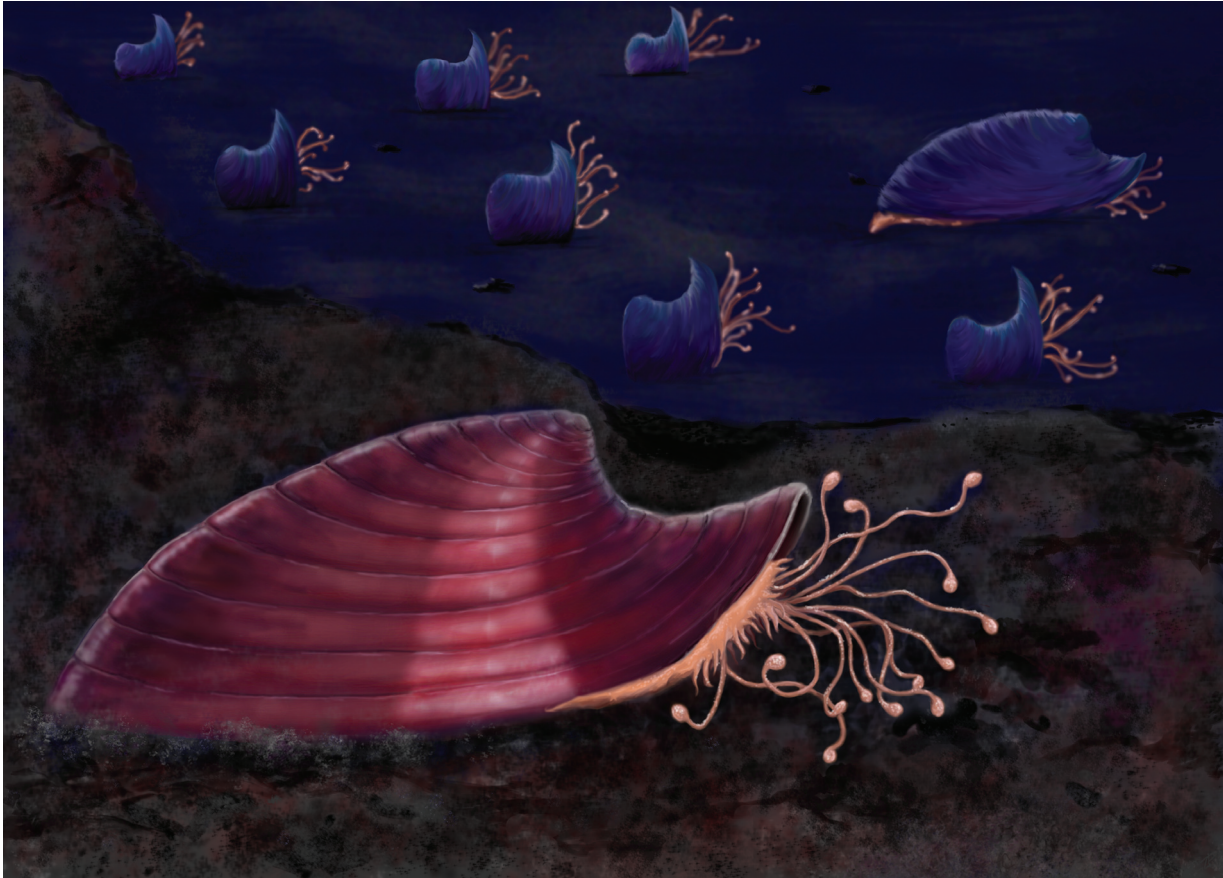
## MATERIALS AND METHODS

The specimens of *Mellopegma georginense* Runnegar and Jell, 1976, *Mellopegma simesi* (MacKinnon 1985) comb. nov., *Mellopegma schizocheras* sp. nov., and *Acanthotheca junior* (Runnegar 1996) gen. nov. described herein are from the Gowers Formation (originally Currant Bush Limestone) in the eastern Georgina Basin, western Queensland, Australia (collected by SMP and A. Knoll in 1998). The localities from which these specimens were collected are shown in Vendrasco et al. (2010, figure 1b). The Gowers Formation has a diverse, exceptionally preserved

phosphatic microfossil assemblage (Shergold and Laurie 1986) with a rich molluscan fauna (Runnegar and Jell 1976). *Mellopegma* is by far the most common mollusc and often the most conspicuous fossil in many of these beds, co-occurring with the molluscs *Pelagiella*, *Yochelcionella*, *Eotebenna*, *Pseudomyona*, *Protowenella*, and others (Vendrasco et al. 2010).

The specimens of *Mellopegma uslonicum* Parkhaev, 2004 discussed here are from the uppermost Emyaksin Formation, *Bergeroniellus micmacciformis* Biozone of the earliest Botoman Stage, from the eastern flanks of the Anabar Uplift of the Siberian Platform. They are from: sample 1420, locality A-53, right bank of the Bol'shaya Kuonamka River, 1-2 km downstream from the Ulakhan-Tyulen' Brook (Valkov 1975); and sample 7/70, locality 96-7, left bank of the Bol'shaya Kuonamka River, ~ 3 km downstream from the mouth of the Ulakhan-Tyulen' Brook (collected by AVK in 1996).

*Mellopegma indecorum* (Missarzhevsky in Rozanov et al. 1969) has been recovered from a few early Cambrian localities on the Siberian Platform. Specimens from sample 183e (locality 183) were collected by V.E. Savitzky from the Kyndyn Formation that cropped out at the left bank of the Rassokha River, ~ 3.5 km upstream from the Sakha-Yurege Rivulet, northern flanks of the Anabar Uplift, Siberia (Egorova and Savitzky 1969, figure 3). These beds are assigned to the Tommotian Stage, *Dokidocyathus regularis* Biozone (according to Rozanov et al. 1969, p. 144). Specimens from sample M303/2 are from the Pestrotsvet Formation, *Dokidocyathus regularis* Biozone (Rozanov et al. 1969), left bank of the middle Lena River, 14 km downstream from the Malykan River, at the mouth of the Tikirikteekh Brook (Shabanov et al. 2008, p. 67).



**FIGURE 1.** Reconstruction of *Mellopegma* from the Gowers Formation. Overall form and life position based on data described and illustrated herein; color pattern is speculative.

The specimens of *Stenotheca drepanoida* (He and Pei in He et al. 1984) are from the early Cambrian Ajax and Parara Limestones of the Mount Scott Range in the Flinders Ranges, South Australia (collected by B. Runnegar and S. Bengtson), University of New England, Armidale Localities (UNEL) 1876 (=1766C), 1852, and 1874 (Bengtson et al. 1990). The Ajax Limestone likely correlates with the Botoman Stage (Jago et al. 2006; Paterson and Brock 2007). One specimen that may be *S. drepanoida* has been found in Missarzhevsky's collection labeled GIN 3593/540, locality indicated as middle Lena River, probably locality M303/2 (Rozanov et al. 1969).

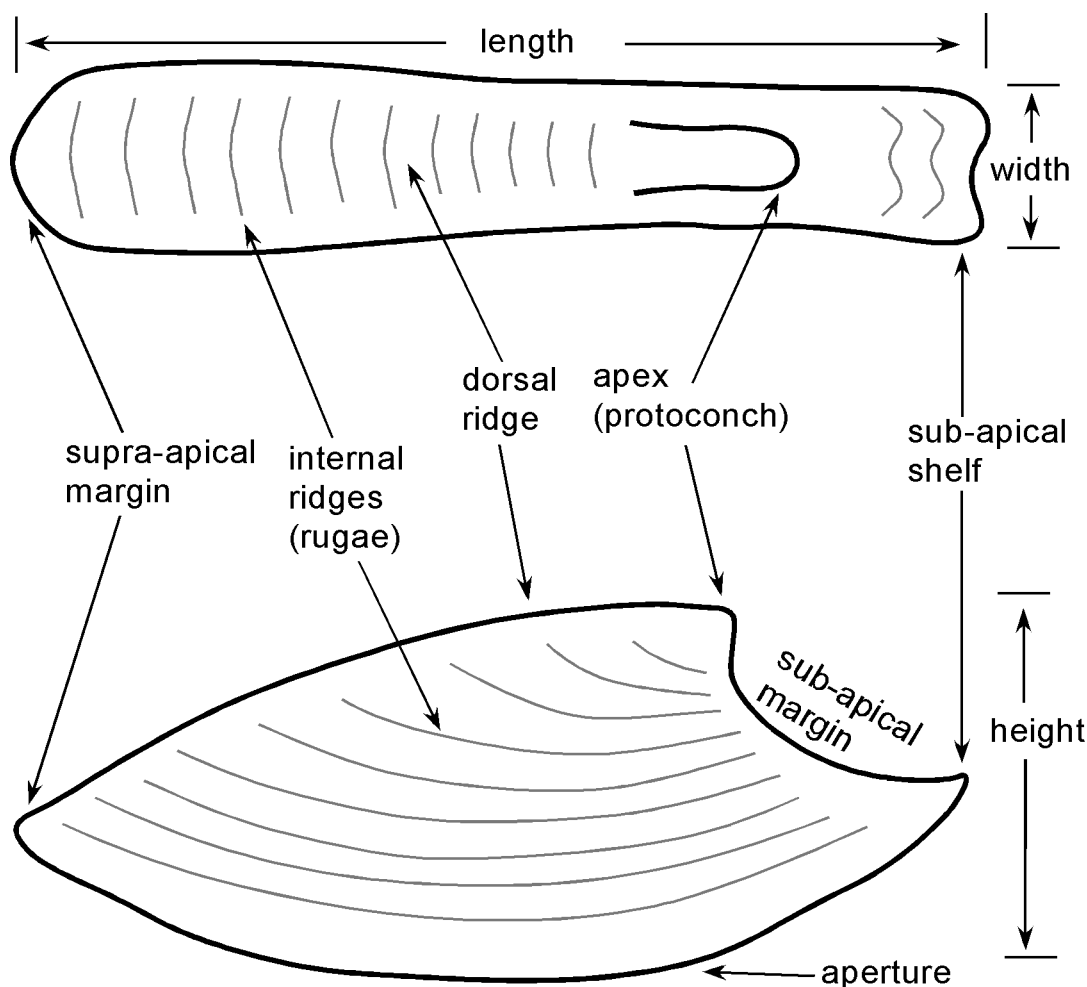
The specimens of *Mellopegma georginense*, *M. simesi*, *M. schizoceras*, and *Acanthotheca junior* from the Gowers Formation of Australia were extracted from the carbonate matrix with 10-15% acetic acid, sorted, and placed on SEM stubs. They were gold coated and photographed with a Zeiss EVO XVP scanning electron microscope (SEM) at the Santa Barbara Museum of Natural History (SBMNH). Specimens of *Mellopegma*

*uslonicum* and *Mellopegma indecorum* were obtained from the collections of V.V. Missarzhevsky, V.E. Savitzky, A.K. Valkov, and AVK, having been isolated from the limestone matrix with a buffered solution of ~10% acetic acid, gold coated, and photographed with a Hitachi S-4300 FE-SEM at the Swedish Museum of Natural History (SMNH). Specimens of *S. drepanoida* were sorted from acid macerates processed by B. Runnegar and S. Bengtson and were examined via the two microscopes listed above.

Images were taken at a variety of voltages (15–30 kV; higher voltage used at greater magnification), typically using secondary electron detectors but occasionally backscatter or variable pressure detectors when charging occurred. Measurements were made from digital SEM photographs using ImageJ (Rasband 1997–2009).

All specimens of *Mellopegma georginense* Runnegar and Jell, 1976, *M. schizocheras* sp. nov., *M. simesi*, and *Acanthotheca junior* gen. nov. are deposited at the Commonwealth Palaeontological Collections (CPC), Geoscience Australia, Can-





**FIGURE 2.** Labelled internal mould and shell replacement of *Mellopegma*, highlighting key anatomical features and terms used herein.

berra. Specimens of *M. indecorum* (Missarzhevsky in Rozanov et al. 1969), *S. drepanoida* and *M. uslonicum* are deposited at the Swedish Museum of Natural History (SMNH).

The analyses of damage and repair frequencies in stenothechids through time were based on three datasets. The first consisted of data from specimens of *Stenothecha* Salter in Hicks, 1872 and *Anabarella* Vostokova, 1962 from the early Cambrian Parara Limestone localities L1763C, L1852, and L1853, South Australia (Bengtson et al. 1990). Samples from these localities were combined so that the number of specimens would be roughly comparable to those from the other two datasets. Damage proportions for each sample were the same as that for the composite sample, so this approach should not affect the analysis. The second and third datasets consisted of *Mellopegma* specimens collected from a bed at the base of the middle Cambrian Gowars Formation, Queensland,

and a bed about 50 cm above it. The one tail z-test for significance of results was performed using online software from Dimension Research (<http://www.dimensionresearch.com/resources/calculators/ztest.html>).

The cladistic analysis was constructed with PAUP 4.0b10 (Swofford 2002). All 21 characters were weighted equally and all character states unordered. *Oelandiella korobkovi* Vostokova, 1962 was used as the outgroup because its shell morphology is well known, it is the oldest helcionellid from Siberia (Gubanov and Peel 1999), and it is somewhat laterally compressed (although not to the same extent as in stenothechids) and thus it may represent the ancestral state of stenothechids. An exhaustive search was completed using maximum parsimony.

The typical form of *Mellopegma* and the key terms used here are illustrated in Figure 2.

**SYSTEMATIC PALAEOLOGY**

Phylum MOLLUSCA Cuvier, 1797

Family STENOHECIDAE Runnegar and Jell,  
1980

**Diagnosis.** Laterally compressed univalves with slight to extensive curvature of the ventral aperture margin.

**Remarks.** Includes *Stenotheca* Salter in Hicks, 1872, *Mellopegma* Runnegar and Jell, 1976, *Eurekapegma* MacKinnon, 1985, and *Acanthotheca* gen. nov.

Parkhaev (in Gravestock et al. 2001) placed *Watsonella* within the Family Stenotheidae. However, the split shell of *Watsonella* (Dzik 1994) excludes it from the stenotheids, which are univalved, although *Watsonella* is surely closely related to stenotheids. *Anabarella* Vostokova, 1962 has been considered a member of the Stenotheidae (Runnegar and Jell 1980; Parkhaev in Gravestock et al. 2001), but *Anabarella plana*, the type species of *Anabarella*, is more similar to *Watsonella* in overall form, shell microstructure, and age (Kouchinsky 1999) than it is to other stenotheids. Therefore, we tentatively exclude *Anabarella* from the Stenotheidae. To complicate matters, the form named *Anabarella australis* Runnegar in Bengtson et al., 1990 is clearly a stenotheid, bearing striking similarities in form to *Stenotheca* and *Mellopegma*. Further taxonomic revision is needed.

The type species of *Anabarella*, *A. plana* Vostokova, 1962, has a greater degree of coiling than other stenotheids (Gubanov and Peel 2003), and we view this trait as the distinguishing characteristic of *Anabarella*. *Mellopegma* differs from other stenotheids in being the most elongate form (typical  $l/w = 4$ ) without a zygion; *Eurekapegma* is similar to *Mellopegma* but possesses a zygion; *Stenotheca* is the only stenotheid that is both tall and narrow; and *Acanthotheca* is the widest and has the greatest ratio of height to length.

The life orientation of the shell in many Cambrian 'monoplacophorans' has been debated, with Peel (1991a, b) having suggested that a large group of these fossils (placed in his Class Helcionelloida) had a shell coiled toward the posterior (endogastric), different from modern monoplacophorans where the shell coils toward the anterior (exogastric). Runnegar and Jell (1980) had previously defined the Family Stenotheidae as exogastric. Runnegar (1996) questioned the basis of Peel's interpretation, in particular inferring an evolutionary link between stenotheids and bivalves

that would indicate the long dorsal margin of stenotheids like *Mellopegma* is homologous to the bivalve ligament. If true, stenotheids would have been exogastric. However, without distinct soft part data for most of these forms it is difficult to know with high certainty which are endogastric and which are exogastric.

Peel (1991b) argued that forms like *Mellopegma* must have been endogastric, with their short, subapical end posterior (and hence in an opposite orientation from bivalves), and that such animals were ancestral to the Class Helcionelloida which he concluded was likewise endogastric. Waller (1998) agreed with others (Runnegar and Pojeta 1974; Pojeta 1978; Runnegar 1978, 1996) in concluding that *Mellopegma* was exogastric, and placed laterally compressed forms such as *Anabarella* and *Mellopegma* in the Class Stenotheidae, separating them from the helcionellids. Others (e.g., Landing and Bartowski 1996, Brock 1998) classified stenotheids in the Class Helcionelloida. Wagner's (1997) cladistic analysis (Figure 3) supports derivation of stenotheids from (other) helcionellids, but our tree (Figure 4) is only consistent with some helcionellids being distant ancestors of stenotheids. Because of the many uncertainties and differing views of the Class Helcionelloida *sensu* Peel (1991a, b)—and even of helcionellids *sensu lato*—we view the classification of stenotheids relative to the Helcionelloida as uncertain.

The defining characteristics of this family are reflected in the cladistic analysis herein as follows: lateral compression (character 9, state 1); univalve (character 8, state 0), and curvature of ventral aperture margin (character 7, state 1; Appendix 1).

Stenotheids may include the ancestors of bivalves and rostroconchs.

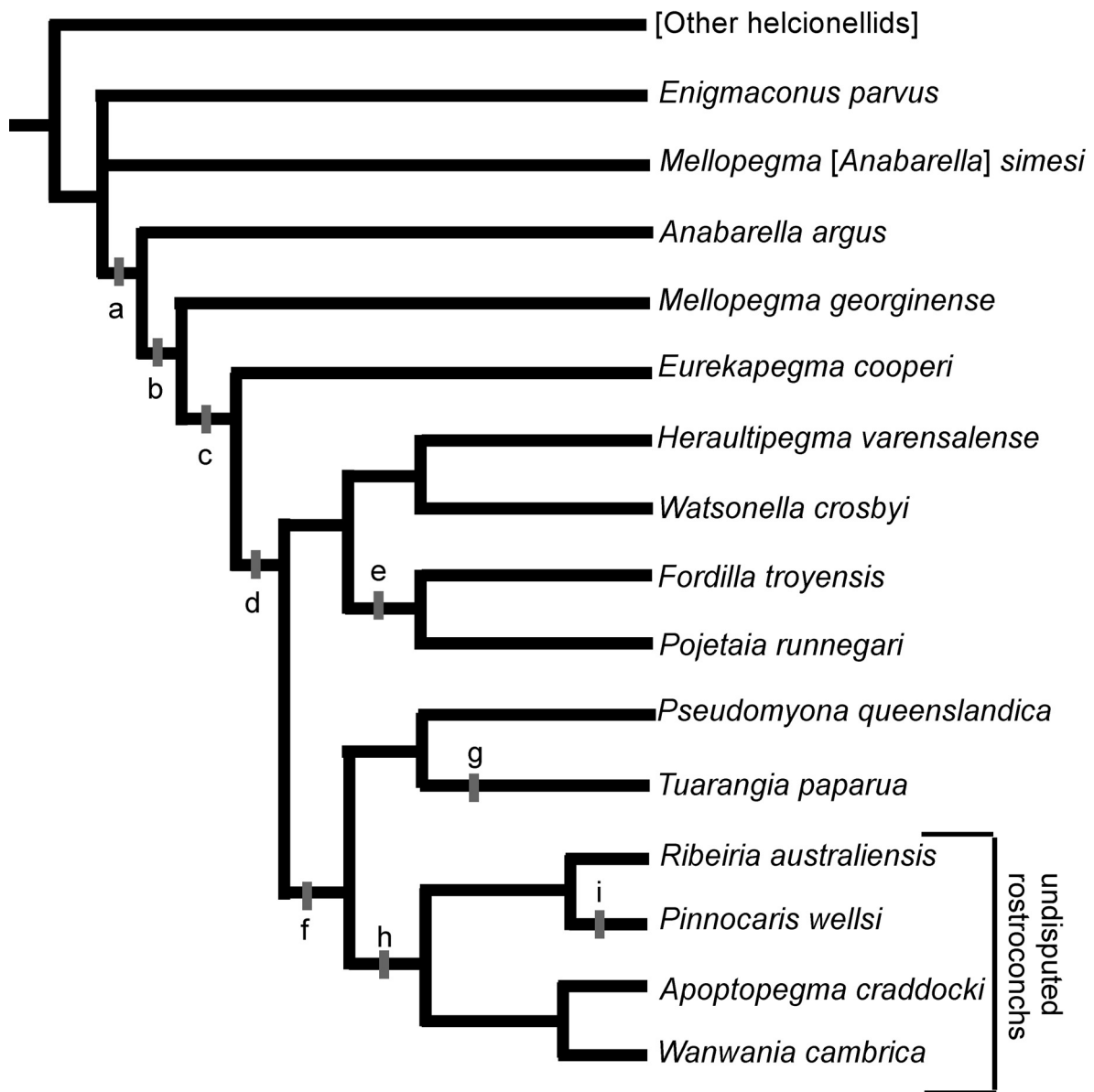
Genus MELLOPEGMA Runnegar and Jell, 1976

**Type species.** *Mellopegma georginense* Runnegar and Jell, 1976.

**Other species.** *Mellopegma indecorum* (Missarzhevsky in Rozanov et al., 1969), *Mellopegma schizocheras* sp. nov., *Mellopegma simesi* (MacKinnon, 1985), and *Mellopegma uslonicum* (Parkhaev, 2004).

**Diagnosis.** Stenotheid molluscs with elongate shells (typical  $l/w > 4$ ) that lack a zygion and possess a strongly curved ventral margin.

**Description.** Laterally compressed, elongate univalves with strongly curved ventral (aperture) margin. Slight coiling (less than half a whorl; cladistic character 4, state 0; Appendix 1), with gently convex supra-apical dorsal margin and concave sub-

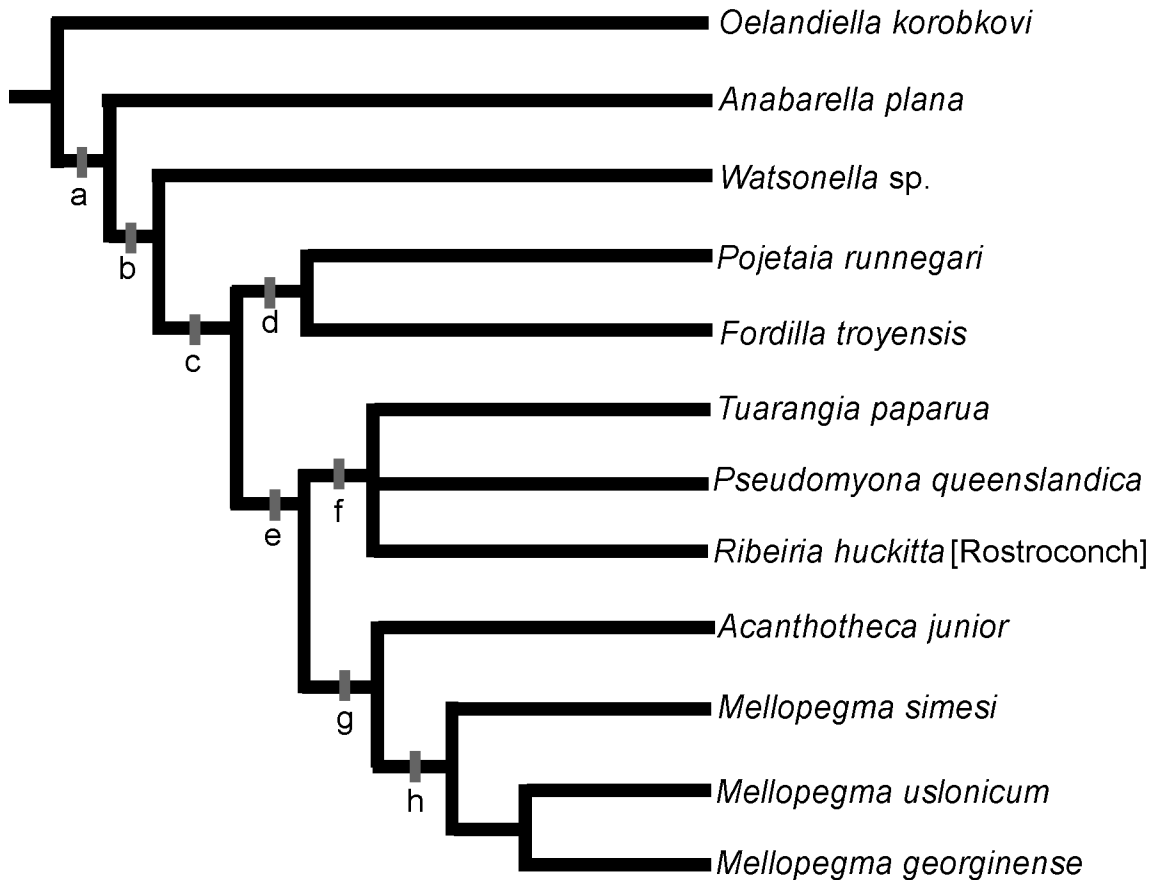


**FIGURE 3.** Copy of a portion of the outgroup analysis in Wagner (1997, figure 3), showing the inferred relationships between *Mellopegma* and *Eurekapegma* ('pararostroconchs' sensu Runnegar 1978), disputed rostroconchs (*Watsonella*, *Pseudomyona*, *Tuarangia*) and undisputed rostroconchs. See text for details. Letters indicate character transitions that are here added to Wagner's (1997) cladogram; see key below. The characters are derived from Wagner's data matrix ([www.treebase.org](http://www.treebase.org)), using the most parsimonious character distribution on his majority-rule consensus cladogram. Key: a, posterior trend projected adapically; b, posterior extension (rostrum) and aperture behind vector from apex; c, posterior gape; d, greatest width not at aperture; e, 2 valves; f, denticles; g, 2 valves; h, H:W=4; i, loss of denticles.

apical margin that ends in a flat to downward-sloping shelf. Shell microstructure of outer layer prismatic and inner layer calcitic semi-nacre (character 17, state 1). Tubercles (granules) occur sporadically on surface of internal moulds, revealing shell pores that extend through most or all of the thickness of the shell (character 14, state 1). Inner

sculpture of gentle to prominent comarginal ridges (character 6, state 1).

**Remarks.** The genus name *Mellopegma* is neuter gender because the ending word, *pegma*, Greek for fastened or thick, is neuter. The gender of all adjective-based species names should be modified to be in agreement with the gender of the genus



**FIGURE 4.** Strict consensus tree of the 3 most parsimonious trees resulting from cladistic analysis herein, showing inferred relationships among stenothecids, bivalves and rostroconchs. Data matrix in Table 3; characters and character states listed in Table 4. Letters indicate character transitions. Key: a, pegma or pegma-like structure, curved ventral margin, lateral compression, laminar inner shell layer; b, reduced shell coiling; c, loss of spiny (lamello-fibrillar) shell microstructure; d, loss of pegma; e, raised sub-apical lip; f, straight dorsal margin, sub-apical width greatest; g, calcitic semi-nacre (or similar) inner shell layer; h, prominent shell pores, aperture constriction near sub-apical margin.

name (International Code of Zoological Nomenclature, ICZN, 34.2). Therefore, we herein carry out justified emendations mandated by the ICZN in modifying the following names of species assigned to *Mellopegma*: *M. georginensis* Runnegar and Jell, 1976 becomes *M. georginense*; *M. indecora* (Missarzhevsky, 1989) becomes *M. indecorum*; and *M. uslonica* Parkhaev, 2004 becomes *M. uslonicum*.

The type species of *Mellopegma*, *M. georginense* Runnegar and Jell, 1976, was defined from numerous internal moulds of laterally-compressed shells from the middle Cambrian Gowars Formation of the Georgina Basin, Australia.

Zhou and Xiao (1984) described *Mellopegma nana* from the early Cambrian of northern China and South Australia, although Parkhaev (in Gravestock et al. 2001) reassigned this species to the

genus *Figurina*. Zhou and Xiao (1984) also named *Mellopegma rostratum*, which was reassigned to *Mackinnonia* by Parkhaev (in Gravestock et al. 2001), an assignment supported by Skovsted (2004), Wotte (2006), and Wagner (2008). The photographs in Zhou and Xiao (1984, figures 3.7-11) support both reassignments.

MacKinnon (1985) described *Eurekapegma*, a form that he argued was very similar to *Mellopegma* except that the former had an internal plate between the lateral walls that he termed a zygion. Based on the great similarity between these two genera, and the fact that *Mellopegma* is slightly older than *Eurekapegma*, MacKinnon (1985) suggested that the former may have given rise to the latter. Whether the presence of the zygion warrants classification in a separate genus is subjective, but it is clear that *Eurekapegma* coo-

*peri* MacKinnon, 1985 is closely related to the species of *Mellopegma* and may have been a descendent of *M. schizocheras* sp. nov.

*Mellopegma* differs from *Anabarella* Vostokova, 1962 in that it is less coiled, has a pronounced sub-apical shelf, and has greater curvature of the aperture margin. *Mellopegma* differs from *Stenotheca* Hicks, 1872 in that it has a greater ratio of length to height, and typically has a more pronounced sub-apical shelf. *Mellopegma* differs from *Watsonella* in having an undivided shell with a lower ratio of height to length.

A summary of the taxonomic history of *Mellopegma* is provided in Table 1.

**Range.** Early to middle Cambrian.

**Occurrence.** Australia, New Zealand, Russia, and Canada.

*Mellopegma georginense* Runnegar and Jell, 1976  
Figures 5-6, 7.3-4

1976 *Mellopegma georginensis* Runnegar and Jell, p. 130, fig. 8b1, 7, 9-11.

2002 *Mellopegma georginensis*; Landing, Geyer, and Bartowski p. 298, fig. 8.1-2.

**Diagnosis.** Laterally compressed, elongate shell with prominent comarginal ridges that continue around the anterior and posterior margins. Supra-apical dorsal margin gently to strongly convex. Sub-apical margin strongly concave, terminating in a flat to downward sloped shelf. Internal moulds covered with regularly spaced pores and ropy comarginal ridges.

**Description.** Shell elongate, laterally compressed, 2-3 times longer than tall (character 10, state 1); 5-7 times longer than wide. Aperture narrow at mid-point (character 20, state 1); widened at either end; upturned at both sub-apical and supra-apical ends. Apex located close to most distal point of sub-apical margin (~20% of shell length); short part of dorsum sharply concave; long part of dorsum mildly convex. Inner shell texture of coarse comarginal rugae; often with fine, sinuous striations. Periostracum with curved ridges that extend from the apex to the aperture. Tubercles (granules) common on internal moulds and in some specimens occur over entire surface. Innermost shell layer consists of highly organized calcitic seminaacre; outer shell layer prismatic (character 11, state 1), with thick-walled organic (conchiolin) matrix. Prismatic shell layer expressed over much of surface of internal mould, except at and near apex. Juveniles slightly less elongate than adults.

**Remarks.** The specimens of *Mellopegma georginense* shown herein are from a locality in the Georgina Basin about 300 km from the type locality (Gowers Formation in both cases). This species is dominant in many of the beds of the Gowers Formation.

The granules shown in Runnegar and Jell (1976, figure 8.b.6) are regularly spaced, but are most likely a line of pore fillings that commonly parallels growth lines in internal moulds of *Mellopegma georginense* and *Mellopegma schizocheras* sp. nov.

Two pyritic steinkerns from the latest early Cambrian of Quebec, Canada, were assigned to *M. georginense* (Landing et al. 2002, figures 8.1-2), and those authors reassigned a fragmented specimen of *Stenotheca?* from the late early Cambrian of New York (Landing and Bartowski 1996, figures 6.1-2, 11.1) to this species. The specimens in Landing et al. (2002) are incomplete but show the same internal ridging, protoconch form, and sub-apical margin as *Mellopegma georginense*, and so assignment to this species is not questioned.

See remarks in descriptions of other species for distinction from *M. georginense*.

**Range.** Early to middle Cambrian.

**Occurrence.** Middle Cambrian Gowers Formation, Georgina Basin, Australia and early Cambrian "Anse Maranda Formation," Québec, Canada.

*Mellopegma schizocheras* sp. nov.  
Figures 7.1-2, 8-9

.1976 *Mellopegma georginensis* Runnegar and Jell, fig. 8b2-5 only.

.1983 *Mellopegma georginensis*; Runnegar, fig. 4b.

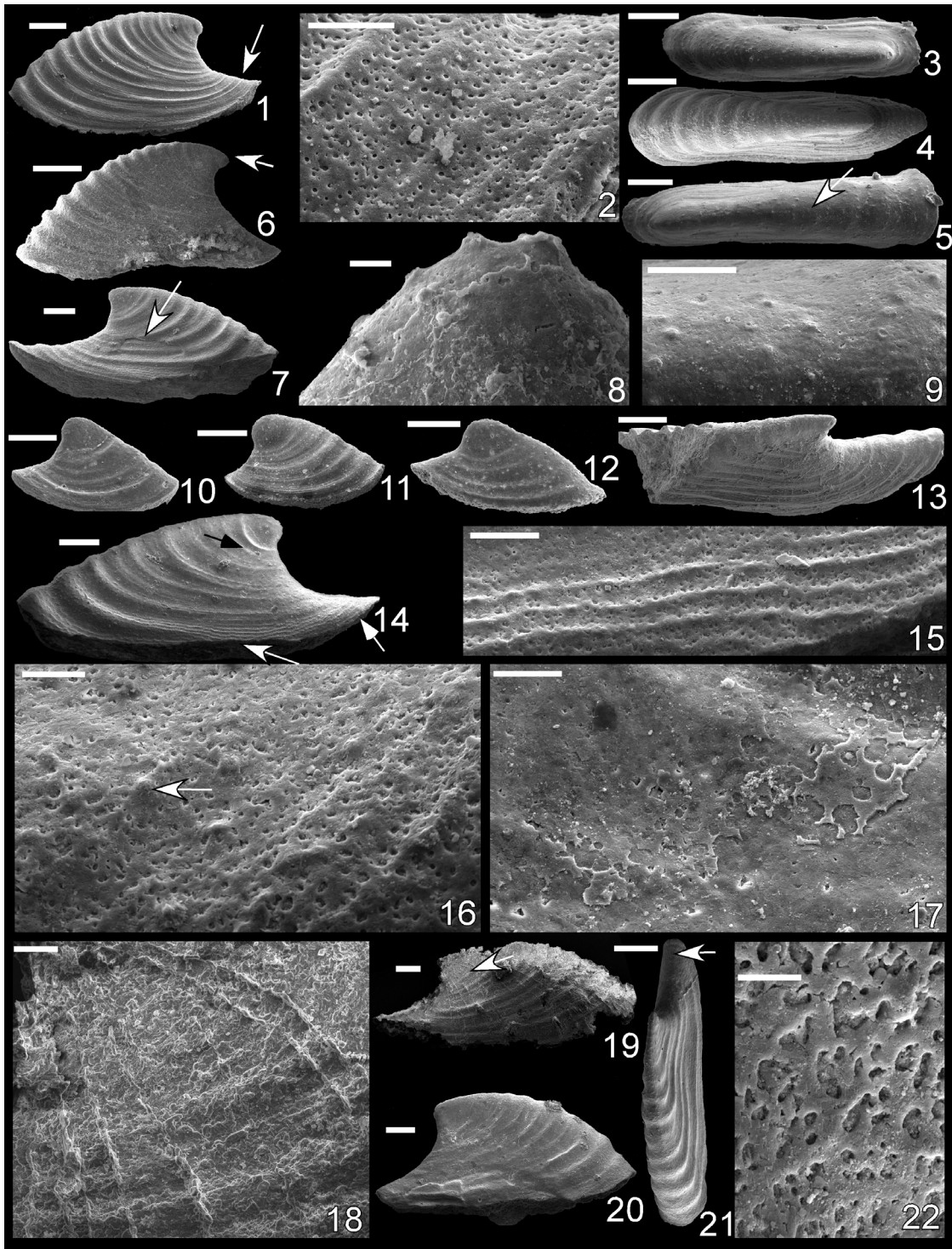
**Etymology.** From the Greek *schizo*, to split or cleave, and *cheras*, silt. The small, blade-like shape of this species would have allowed it to easily navigate (or slice) through interstitial sediment.

**Material.** Holotype (Figure 8.1; CPC 40456), three paratypes (Figure 8.8, 10, 15; CPC 40464, 40465, 40470), and numerous other specimens from near the type locality.

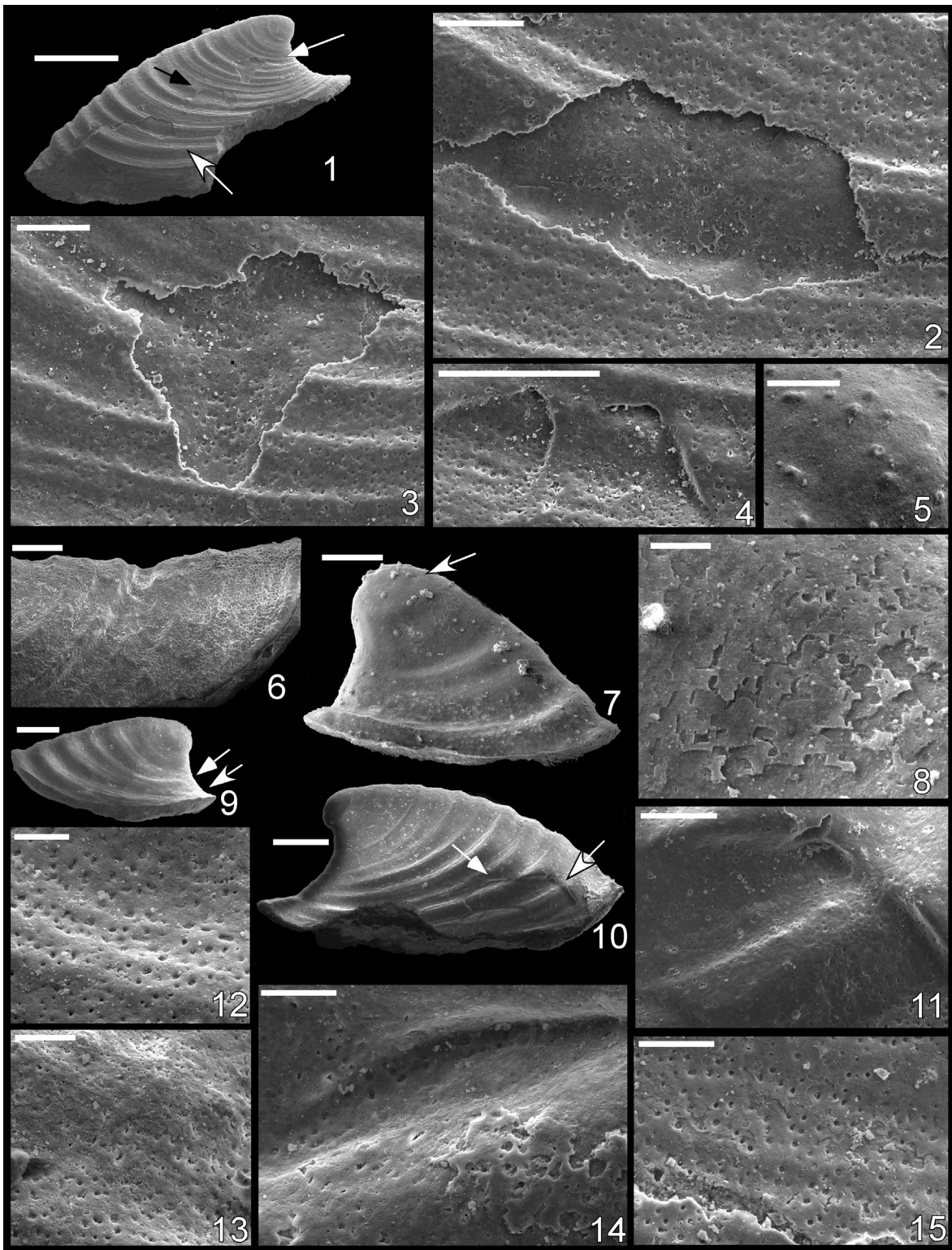
**Type locality.** Just above the Bronco Stromatolith Bed of the Gowers Formation, c. 200 m East-Northeast along strike from section 415 (see Shergold and Southgate 1986, Southgate 1986, and Vendrasco et al. 2010).

**Diagnosis.** Shell elongate, highly laterally compressed, typically with faint comarginal rugae. Dorsal supra-apical margin gently convex. Sub-apical margin concave, terminating in short shelf. Pris-

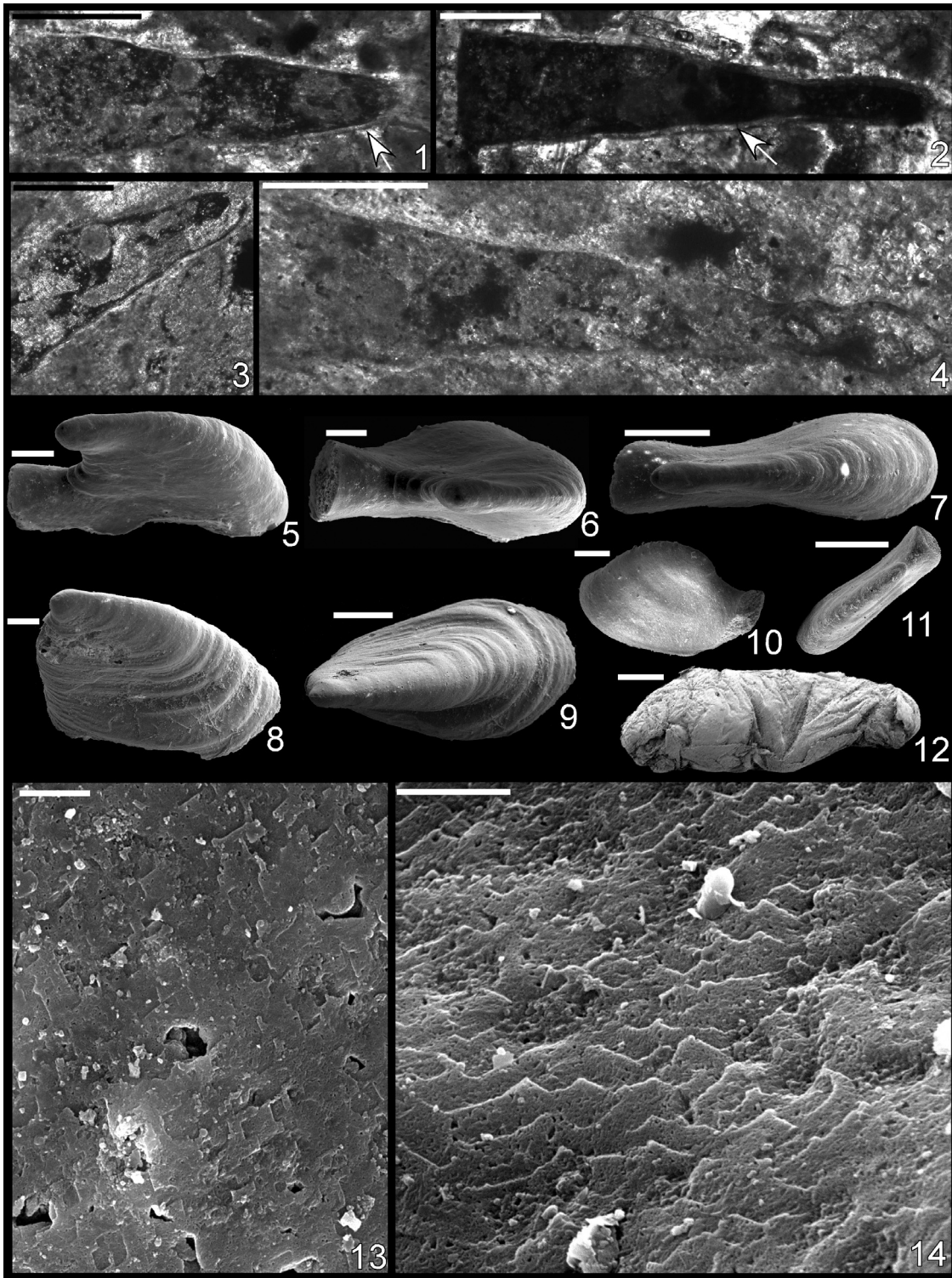




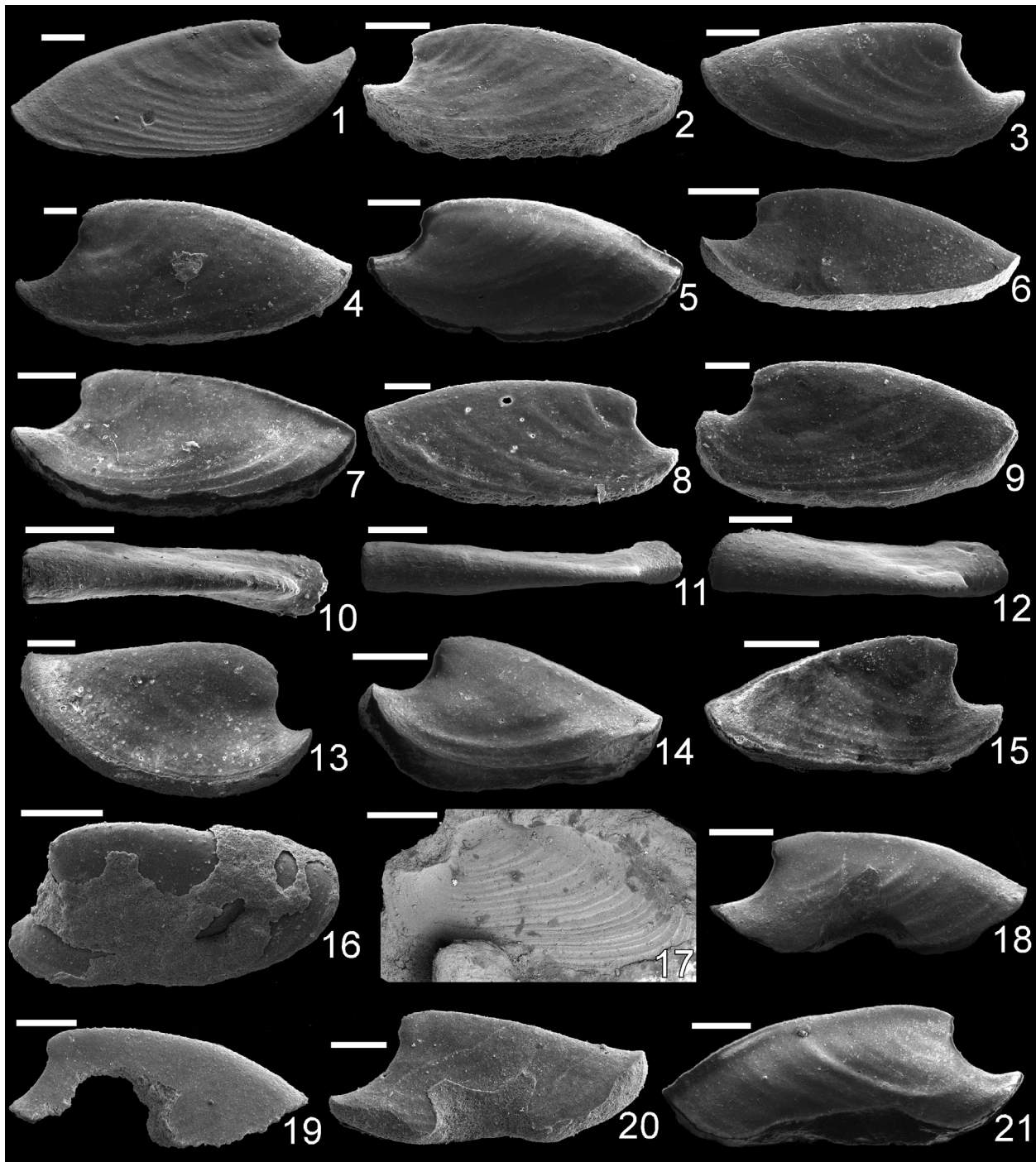
**FIGURE 5.** *Mellopegma georginense* Runnegar and Jell, 1976 from the middle Cambrian of Australia. 1, 2, CPC 40431; arrow in 1 shows location of 2. 3, CPC 40432. 4, CPC 40433. 5, 9, CPC 40434; arrow in 5 shows location of 9. 6, 8, CPC 40512; arrow in 6 shows location of 8. 7, CPC 40435. Arrow shows imprint of shell scar. 10, CPC 40436, juvenile shell. 11, CPC 40437, juvenile shell. 12, CPC 40438, juvenile shell. 13, CPC 40439. 14-17, CPC 40440; in 14 the barbed arrow shows location of 15, barb-less white arrow shows location of 17, and solid black arrow shows location of 17. In 16, the arrow shows location of tubercle at polygon boundary. 18-19, CPC 40441; arrow in 19 shows location of 18. 20, CPC 40442. 21-22, CPC 40443; arrow in 21 shows location of 22. Scale bars: 1, 6, 500  $\mu$ m; 2, 9, 15, 50  $\mu$ m; 3-4, 7, 10-14, 19-21, 200  $\mu$ m; 5, 100  $\mu$ m; 8, 16-17, 20  $\mu$ m; 18, 50  $\mu$ m; 22, 10  $\mu$ m.



**FIGURE 6.** *Mellopegma georginense* Runnegar and Jell, 1976 from the middle Cambrian of Australia. 1-4, CPC 40444; in 1 the barbed arrow shows location of 2, white barb-less arrow shows location of 3, and solid black arrow shows location of 4. 5, CPC 40445. 6, CPC 40446. 7-8, CPC 40447; arrow in 7 shows location of 8. 9, 12-13, CPC 40448; in 9 the barbed arrow shows the location of 12 and the barb-less arrow shows location of 13. 10-11, 14, CPC 40449; in 10, the barbed arrow shows location of 11, barb-less arrow shows location of 14. 15, CPC 40450. Scale bars: 1, 4, 9-10, 200  $\mu$ m; 2, 5, 11, 15, 50  $\mu$ m; 3, 12-14, 20  $\mu$ m; 6, 7, 100  $\mu$ m; 8, 10  $\mu$ m.

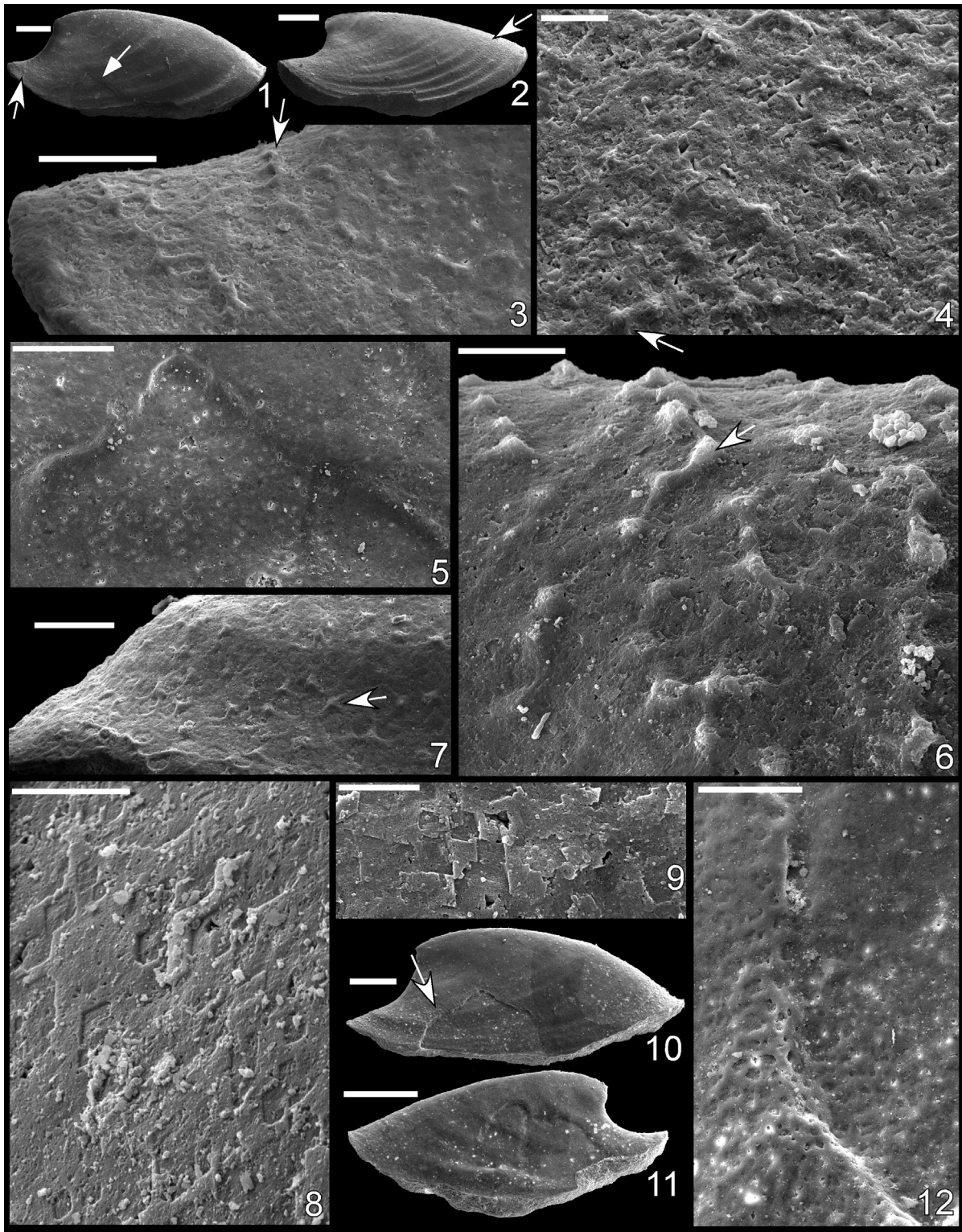


**FIGURE 7.** Thin sections and unusual internal moulds of *Mellopegma* from the Gowers Formation, middle Cambrian, Australia. Specimens 1, 3, 4 on slide CPC 40451. Specimen 2 on slide CPC 40452. 1, 2, thin sections of *Mellopegma schizocheras* sp. nov. Arrows point to thin external phosphate coat covering calcite shell replacement, revealing thickness of original shell. 3, 4, thin sections of *Mellopegma georginense* Runnegar and Jell, 1976. 5-7, internal mould of *Mellopegma* sp., CPC 40453. 8-9, 13-14, internal mould of *Mellopegma*?, CPC 40454. 10-11, internal mould of *Mellopegma schizocheras*?, CPC 40455. 12, possible coprolite that contains a bradoriid shell. Scale bars: 1-4, 7, 9-11, 200 µm; 5-6, 8, 12, 100 µm; 13-14, 5 µm.



**FIGURE 8.** *Mellopegma schizocheras* sp. nov. from the middle Cambrian of Australia. 1, holotype, CPC 40456. 2, CPC 40457. 3, CPC 40458. 4, CPC 40459. 5, CPC 40460. 6, CPC 40461. 7, CPC 40462. 8, paratype, CPC 40463. 9, CPC 40464. 10, paratype, CPC 40465. 11, CPC 40466. 12, CPC 40467. 13, CPC 40468. 14, CPC 40469. 15, paratype, CPC 40470. 16, CPC 40471. 17, external mould, CPC 40472. 18, CPC 40473. 19, CPC 40474. 20, CPC 40475. 21, CPC 40476. Scale bars: 1-3, 5-8, 10-12, 14-21, 200  $\mu$ m; 4, 9, 13, 100  $\mu$ m.





**FIGURE 9.** *Mellopegma schizocheras* sp. nov. from the middle Cambrian of Australia. 1, 3, 5, CPC 40477; in 1 the barbed arrow shows location of 3, barb-less arrow shows location of 5. In 3, arrow shows location of tubercle at polygon boundary. 2, 4, CPC 40478; arrow in 2 shows location of 4. In 4, arrow shows location of tubercle at polygon boundary. 6, CPC 40479; arrow shows location of tubercle at polygon boundary. 7, CPC 40480; arrow shows location of tubercle at polygon boundary. 8, CPC 40481. 9, CPC 40482. 10, 12, CPC 39705; arrow in 10 shows location of 12. 11, CPC 40483. Scale bars: 1-2, 10-11, 200  $\mu$ m; 3, 5-6, 50  $\mu$ m; 4, 20  $\mu$ m; 7, 12, 100 $\mu$ m; 8-9, 10  $\mu$ m.



matic shell microstructure occasionally preserved as polygons on internal moulds near the anterior and posterior aperture margin.

**Description.** Elongate, laterally compressed univalve with faint internal ridges on the internal mould. The internal ridges roughly parallel the growth lines and fade out near the anterior and posterior margins. These ridges vary in this species in depth, spacing, and number. Dorsal margin broadly convex, sub-apical margin concave with extended shelf. Tubercles present over much of surface of some internal moulds, but typically most common along the dorsal margin, including the apex, and along the internal ridges. Polygonal texture on sub-apical lip of many specimens, probably representing prismatic shell microstructure of outer shell layer. Angular texture with imprints of parallelogram-shaped tablets occur on all other regions of internal moulds, representing highly organized version of calcitic semi-nacre. The angular imprints are visible in various states of preservation on all specimens examined. Many specimens had an internal thickening parallel to, and just below, dorsum (Figure 8.5, 8.7, 8.21).

**Remarks.** This species differs from *Mellopegma georginense*, with which it co-occurs, in having a more dorso-ventrally compressed, elongate shell with less distinct internal rugae. These rugae are present along the dorsal ridge of the internal moulds of *M. georginense*, whereas they thin out at the dorsal ridge of *Mellopegma schizocheras* sp. nov. Specimens of *M. schizocheras* tend to be more elongate than those of *M. georginense* (compare Figure 5.3-5 with Figure 8.10-12), although some specimens of *M. georginense* are also elongate (Figure 5.21). The polygonal texture differs dramatically between these two species: in *M. georginense* the polygons are thick walled, with a small diameter, and occur over much of the surface of the internal mould (Figures 5.2, 5.16, 5.22, 6.12, 6.15); in *M. schizocheras* sp. nov. the polygons are thin walled, with a larger diameter, and occur near the aperture margin at and near the anterior or posterior edge of the internal mould (Figure 9.3). The size overlap of these two species, as well as the form of juveniles deduced from small specimens (Figures 5.10-12, 6.7, 6.9, 8.13-15) and growth lines in adults reveal that these two morphotypes are not different ontogenetic stages of the same animal. Moreover, this does not appear to be a case of sexual dimorphism, as juveniles of both morphs look different.

See remarks in descriptions of following *Mellopegma* species for distinction from *M. schizocheras*.

**Range.** Middle Cambrian (Floran).

**Occurrence.** Only from Gowers Formation in the Thornton region of the Georgina Basin, Australia.

*Mellopegma simesi* (MacKinnon, 1985) comb. nov.  
Figures 10-11

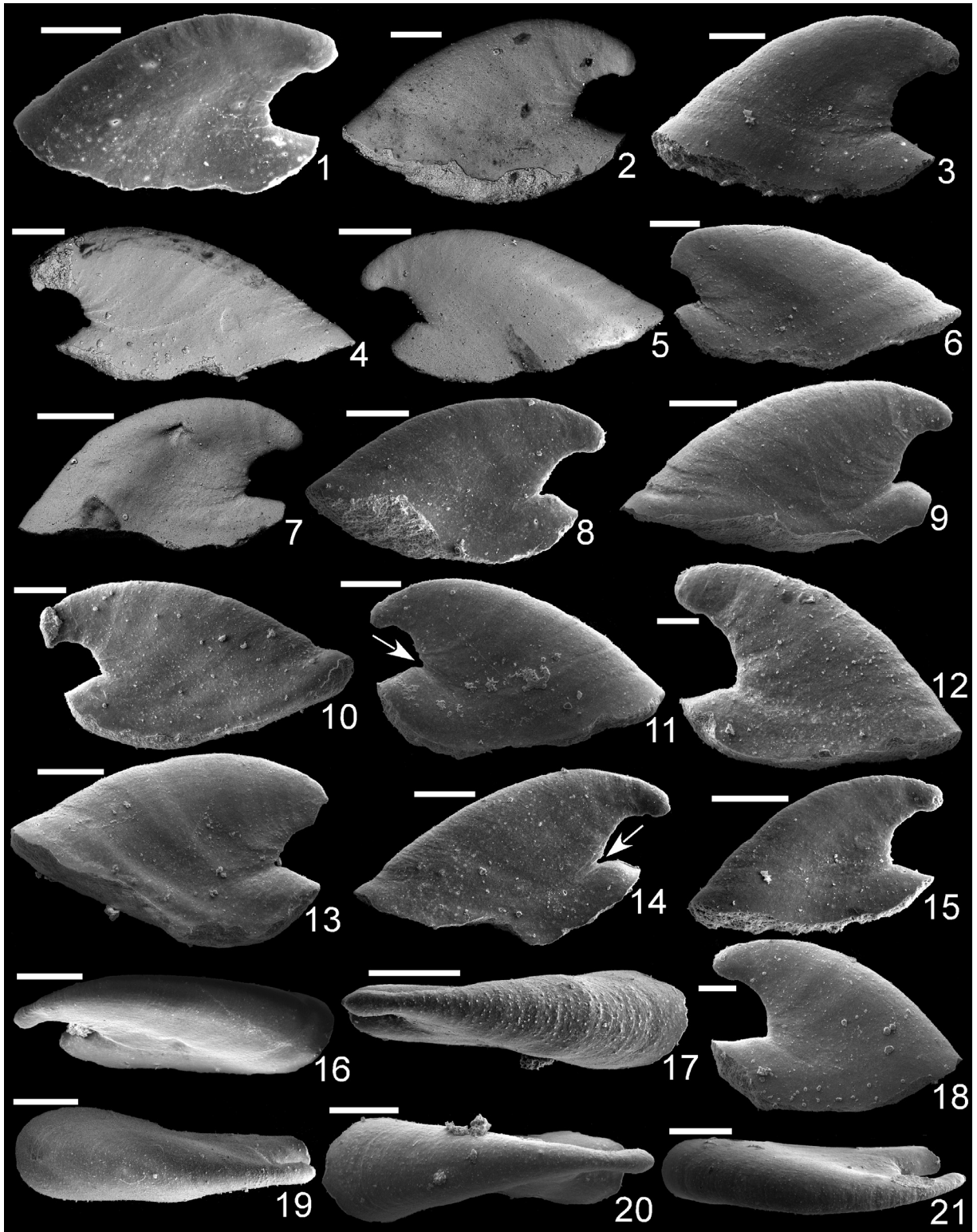
.1976 *Mellopegma georginensis* Runnegar and Jell, fig. 8b12-13 only.

.1985 *Anabarella simesi* MacKinnon, p. 71, fig. 3a-j.

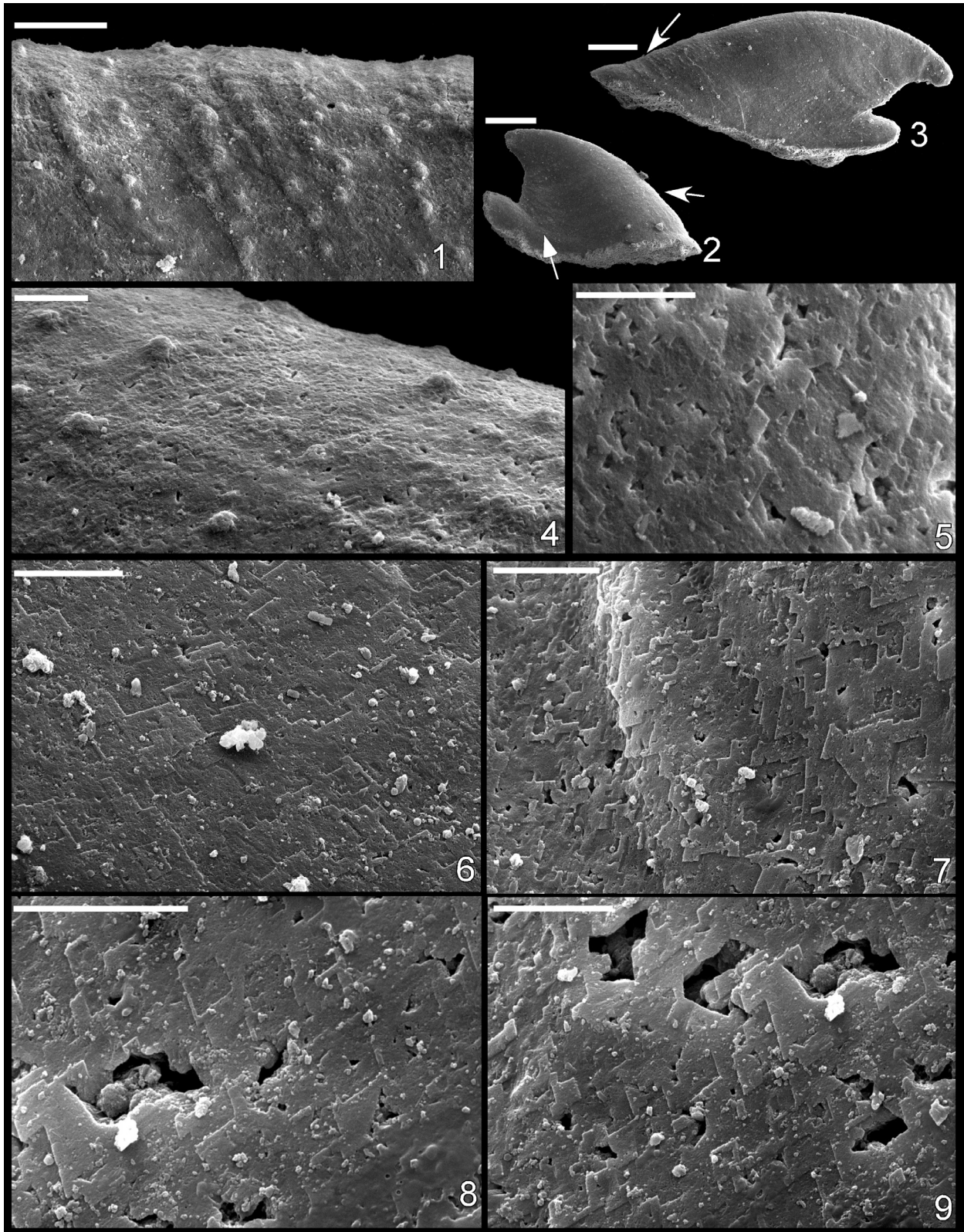
**Description.** Laterally compressed, elongate shell with less than half a coil. Margin below apex strongly concave; dorsal margin weakly to strongly convex. Faint internal ridges on some specimens. Raised sub-apical margin, forming a shelf ranging from nearly horizontal to angling downward at 45°. Supra-apical margin tends to be wider than sub-apical margin (Figure 10.17, 10.19-20; cladistic character 21, state 1; Appendix 1). Granules apparent in some internal moulds, paralleling growth lines (Figures 10.17, 11.1). Prominent protoconch (Figure 10.12, 10.17) bulbous. Pegma or pegma-like structure developed to varying degrees (Figures 10, 11.2-3; character 1, state 1).

**Remarks.** This species was originally considered to be a member of *Anabarella*, but it shares more distinguishing characters with the type species of *Mellopegma* (*M. georginense* Runnegar and Jell, 1976) than the type species of *Anabarella* (*A. plana* Vostokova, 1962). In particular, the lesser degree of coiling and flared sub-apical margin readily distinguish *Mellopegma* (including *M. simesi* comb. nov.) from *Anabarella*. In addition, *Mellopegma simesi* shares with *M. georginense* identical patterns and shapes of shell pores (Figures 10.17, 11.1, 11.4) and inner shell microstructure (Figure 11.5-9). In contrast, there is no evidence for pores in *Anabarella plana*, and it had a much different pattern of shell microstructure (compare Figure 11.5-9 herein with Kouchinsky 1999, figure. 1-2).

*Mellopegma simesi* can be distinguished from all other species of *Mellopegma* in having a more pronounced pegma or pegma-like structure. It also differs from *M. georginense* in having much less prominent internal ridges; from *M. indecorum* and *M. schizocheras* sp. nov. in having a less smoothly rounded sub-apical margin; and from *M. uslonicum* in having a more inset sub-apical region.



**FIGURE 10.** *Mellopegma simesi* (MacKinnon, 1985) comb. nov. from the middle Cambrian of Australia. 1, CPC 40484. 2, CPC 40485. 3, CPC 40486. 4, CPC 40487. 5, CPC 40488. 6, CPC 40489. 7, CPC 40490. 8, CPC 40491. 9, CPC 40492. 10, CPC 40493. 11, CPC 40494; arrow points to greater developed pegma. 12, CPC 40495. 13, CPC 40496. 14, CPC 40497; arrow points to greater developed pegma. 15, CPC 40498. 16, CPC 40499. 17, CPC 39713. 18, CPC 40500. 19, CPC 40501. 20, CPC 40502. 21, CPC 40503. All scale bars 200  $\mu$ m except 12 and 18 with scale bars of 100  $\mu$ m.



**FIGURE 11.** *Mellopegma simesi* (MacKinnon, 1985) comb. nov. from the middle Cambrian of Australia. 1, 3, CPC 40504; arrow in 3 shows location of 1. 2, 4, 5, CPC 40505; arrow in 2 shows location of 4. 6, CPC 39717. 7, CPC 40506. 8-9, CPC 40507 Scale bars: 1, 50  $\mu\text{m}$ ; 2-3, 200  $\mu\text{m}$ ; 4, 20  $\mu\text{m}$ ; 5-9, 10  $\mu\text{m}$ .

There is some uncertainty in assigning this species to *Mellopegma*, primarily due to the presence of two characters of this species not seen in any other species of *Mellopegma*: elongate apical neck (i.e., sharply in-curved sub-apical margin) and abrupt transition between sub-apical surface and shelf. These two characters are seen in specimens of *Anabarella*, but this species differs from *Anabarella* in the ways listed above. *Stenotheca drepanoidea* shares with *M. simesi* a pegma-like structure just above the sub-apical shelf (Parkhaev in Gravestock et al. 2001, pl. xliii, figure 1) and an elongate sub-apical neck. However, *M. simesi* differs from *Stenotheca drepanoidea*—and in fact other species of *Stenotheca*—in having: (1) a more elongate shell; (2) less lateral compression; and (3) greater curvature of the ventral margin. While *M. simesi* has striking similarities with species of *Stenotheca*, *Anabarella*, and *Mellopegma*, current data indicate it shares the greatest similarity with *Mellopegma*, and consequently we classify it as such; this classification is supported by our cladistic analysis (Figure 4). Some of the character states of *M. simesi* not seen in *M. georginense*—including an incurved sub-apical slope and lack of prominent internal ridges—are seen in *M. schizocheras*.

**Range.** Middle Cambrian.

**Occurrence.** Gowers Formation in the Thornton region of the Georgina Basin, Australia and Tasman Formation, New Zealand.

*Mellopegma uslonicum* Parkhaev, 2004  
Figures 12-13

2000a “Unnamed form 3”; Kouchinsky, fig. 5.m-o.

2004 *Mellopegma uslonica* Parkhaev, p. 603, pl. 2, figs. 5-9.

**Description.** Elongate, laterally compressed shell with gently convex dorsal margin and gently concave sub-apical margin with slight lateral flaring of aperture. Internal mould typically covered with tubercles or granules (Figure 13.1, 13.3, 13.4), revealing nearly isotropically spaced cavities or pores along the inner shell surface. External ornament of ridges.

**Remarks.** Parkhaev (2004) named *Mellopegma uslonica* (now *M. uslonicum*) for specimens from the early Cambrian (Botoman) of Transbaikalia. These early Cambrian forms differ from the type species in being slightly less compressed laterally and typically less elongate, but otherwise are similar in form to *M. georginense*.

This species clearly belongs to *Mellopegma*, as it shares with the type species a similar pore system, significant lateral compression, sharply raised and slightly flared sub-apical margin, and faint internal ridges (Parkhaev 2004, pl. 2, figs. 5-9). The occurrence of this species indicates that *Mellopegma* existed in typical form during the Botoman.

*M. uslonicum* differs from all other known species of *Mellopegma* in having equally spaced pores over the entire inner surface of the shell, and in having a sub-apical margin that is less recessed.

**Range.** Early Cambrian (Botoman).

**Occurrence.** Emyaksin Formation from the eastern flanks of the Anabar Uplift of the Siberian Platform and the Bystraya Formation of the Chita Region, Russia.

*Mellopegma indecorum* (Missarzhevsky in  
Roazanov et al., 1969)  
Figure 14

1969 *Anabarella indecora* Missarzhevsky in Roazanov et al., 1969, p. 144, pl. 4, figs. 7-8.

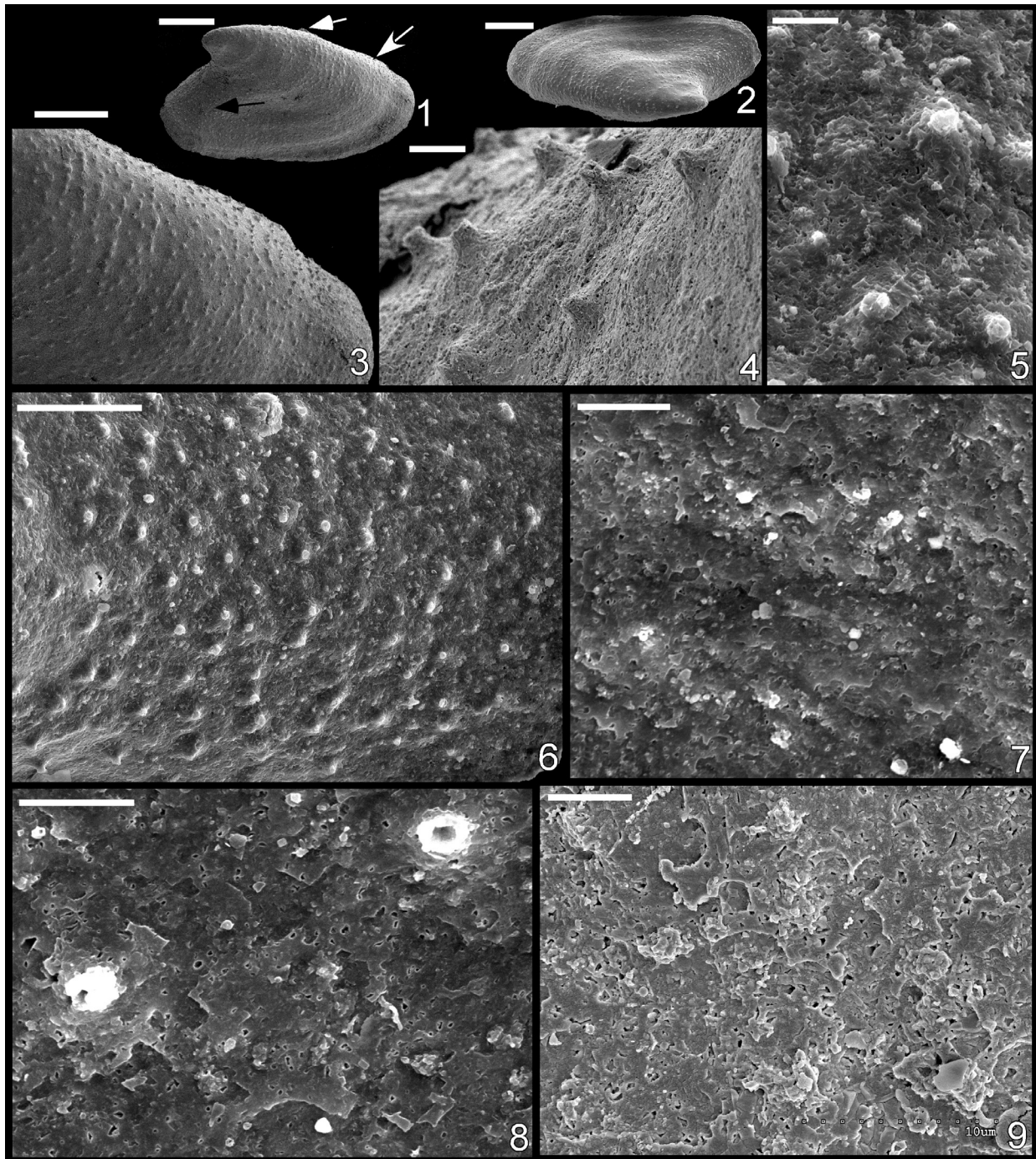
1989 *Mellopegma indecora*; Missarzhevsky, p. 179, pl. 6, figs. 10-11.

**Description.** Shell elongate, laterally compressed in sub-apical region of aperture, laterally expanded to a great degree along rest of aperture. Internal ornament of comarginal rugae. Dorsal margin smoothly convex; sub-apical margin sharply concave (forming an emargination), ending in a prominent sub-apical shelf.

**Remarks.** Missarzhevsky (1989) assigned the name *Mellopegma indecora* (now *M. indecorum*) to specimens from the early Cambrian (Tommotian) of Russia. He had previously assigned this species to the genus *Anabarella* (Missarzhevsky in Roazanov et al. 1969). Parkhaev (2004) recognized *M. indecorum* as a valid species of *Mellopegma*. Although Wagner (2008) classified *M. indecorum* as a species of *Anabarella*, he more recently stated his agreement with Missarzhevsky's and Parkhaev's decision (Wagner, personal commun., 2010).

The specimens of *Mellopegma indecorum* photographed by Missarzhevsky (1989, pl. 6, figs. 10-11) show significant lateral compression and strongly pronounced internal ridges. Although his photographs lack detail, new photos of the specimens in his figure 11 (Figure 14.1-6 here) suggest these are in fact members of *Mellopegma*. In addition, the specimens shown in Missarzhevsky in Roazanov et al. (1969, pl. 4, figs. 7-8) are laterally





**FIGURE 12.** *Mellopegma uslonicum* Parkhaev, 2004. 1-9, SMNH Mo167609; in 1 the barbed arrow shows location of 3, white barb-less arrow shows location of 4, and solid black arrow shows location of 5-9. Scale bars: 1-2, 200 µm; 3-5, 7-8, 10 µm; 6, 50 µm; 9, 5 µm.

compressed and show the internal ridges, curved ventral margin, and upturned sub-apical shelf (character 5, state 1) typical of *Mellopegma*. These features are clearly seen on the holotype of this species (Missarzhevksy *in* Rozanov et al. 1969, pl. 4, fig. 8), and the prominent sub-apical shelf and

lesser coiling it shows are distinct from what characterizes *Anabarella*. We therefore consider *M. indecorum* to be a valid species of *Mellopegma*.

This species appears to belong to *Mellopegma*, as it shares with other species of this genus the same lateral profile, lateral compression



**TABLE 2.** Characteristics of *Mellopegma* that are adaptive in resisting or eluding predatory attacks.**Characters in *Mellopegma* adaptive for defense**

Tiny size  
 Folds in shell  
 Elongation  
 Narrow aperture  
 Burrowing characters:  
   Streamlining of shell  
   Smooth surface  
   Anterior expansion for foot  
 Lightweight shell

in the sub-apical half of the shell, internal ornament of comarginal rugae, and laminar inner shell microstructure. However, this species differs from all other known species of *Mellopegma* in having a much more expanded supra-apical region of the shell (Figure 14.3-4, 14.20). This lateral expansion is similar to what occurs in a few equivocal forms of *Mellopegma* from the middle Cambrian (Figure 7.7, 7.9), although these two unusual specimens differ from *M. indecorum* in having a more pronounced sub-apical shelf in one case (Figure 7.7), and in having a greater amount of expansion and more convex sub-apical margin in the other (Figure 7.9). The occurrence of *M. indecorum* reveals that *Mellopegma* existed during the Tommotian, and that it co-occurred with *Watsonella*. *M. indecorum* is intermediate in extent of lateral compression between non-stenothecid helcionellids and typical stenothecids.

The holotype of *M. indecorum* is listed from sample 183e on p. 144 of Rozanov et al. (1969), but in the caption to pl. IV, fig. 8, on p. 303 the same specimen is attributed to sample M302/1-2 (Rozanov et al. 1969), which is the same age but from the middle Lena River. The holotype and another specimen illustrated by Rozanov et al. (1969, pl. IV, figs. 7-8) appear to be missing from Missarzhevsky's collection at present, but sample 183e yielded two incomplete moulds of *M. indecorum* figured herein (Figure 14.7-12) along with other fossils of Tommotian Age (AVK, personal observation). We conclude that the holotype of *M. indecorum* should be attributed to sample 183e, and that the reference to sample M302/1-2 is a mistake. However, according to Rozanov et al. (1969, p. 145), *M. indecorum* is indeed present in M302/1-2 and also in sample M303/2, the latter

collected by Missarzhevsky from a nearby locality of the same age.

**Range.** Early Cambrian (Tommotian).

**Occurrence.** Kyndyn and Pestrotsvet Formations, Siberian Platform.

*Mellopegma* sp.

Figure 7.5-7

**Remarks.** An unusual specimen of *Mellopegma* from the middle Cambrian Gowers Formation of Australia looks to be intermediate in lateral view between *M. schizocheras* and *M. simesi*, but has a lateral expansion at the supra-apical end of the aperture that is seen in neither. However, a number of characters suggest this is a member of *Mellopegma*, including: lateral compression at sub-apical end, prominent sub-apical shelf, sharply concave sub-apical margin (forming an embayment), gently convex dorsal ridge, and internal ridges.

*Mellopegma?*

Figure 7.8-9, 7.13-14

**Remarks.** One unusual specimen from the middle Cambrian Gowers Formation of Australia has internal ridges and bulbous apex similar to *Mellopegma* spp., and remarkably similar shell microstructure (Figure 7.13) to other members of this species. However, it differs from other species of *Mellopegma* in having a convex, nearly vertical sub-apical margin. Moreover, this specimen shows a high degree of lateral expansion at the aperture, unusual for most species of *Mellopegma* but seen to a lesser extent in *Mellopegma indecorum* (Figure 14.4, 14.16, 14.18).

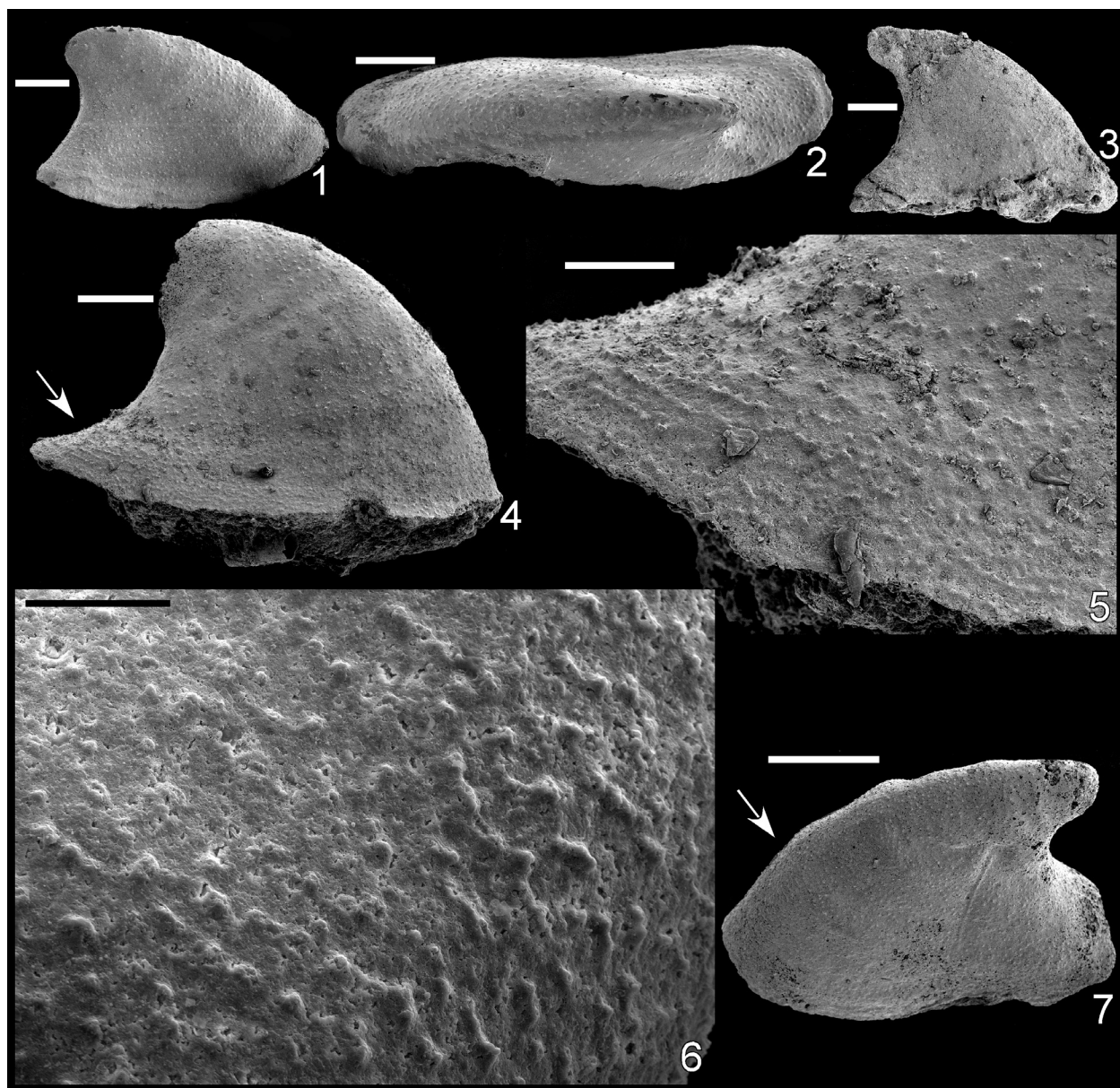
Genus STENOTHECA Salter in Hicks, 1872

**Type species.** *Stenotheca cornucopia* Salter in Hicks, 1872.

**Other species.** *Stenotheca acutacosta* Walcott, 1890, *Stenotheca clotho* Walcott, 1912, *Stenotheca drepanoida* (He and Pei in He et al., 1984), *Stenotheca manchurica* Kobayashi, 1933, *Stenotheca pojetai* Runnegar and Jell, 1976, *Stenotheca tepee* Runnegar and Jell, 1976, and *Stenotheca transbaikalica* Parkhaev, 2004.

**Description.** Highly laterally compressed, tall univalve with a sub-triangular lateral profile, slight coiling (about 1/8 to just over 1/4 one whorl), concave sub-apical margin (embayment) that borders an angular to flat sub-apical shelf.

**Remarks.** The type species is poorly known. One specimen was drawn by Salter (in Hicks 1872), and then three specimens were drawn—with more

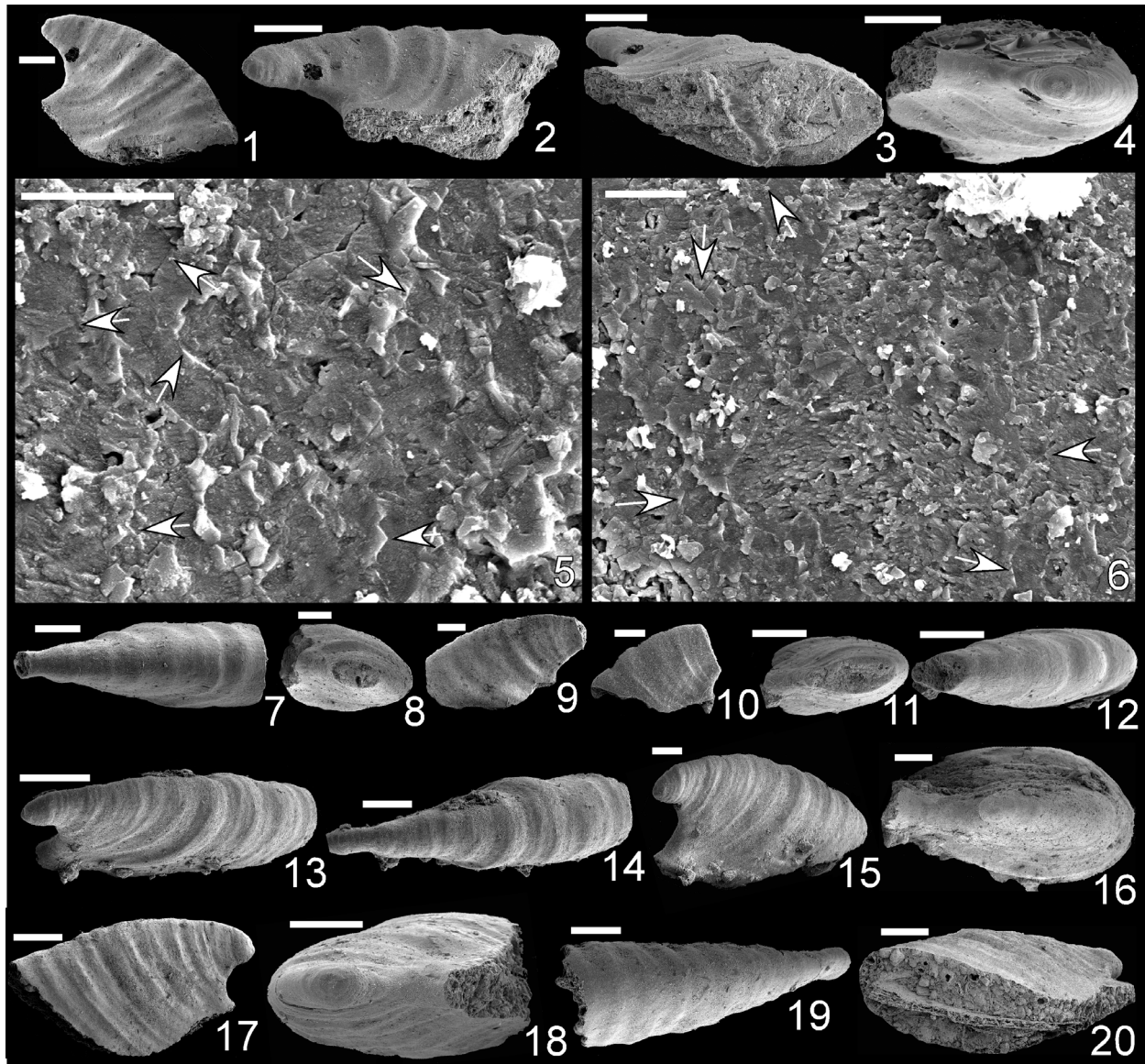


**FIGURE 13.** *Mellopegma uslonicum* Parkhaev, 2004. 1, 2, SMNH Mo167610. 3, SMNH Mo167611. 4, 5, SMNH Mo167612. Arrow in 4 shows location of 5. 6, 7, SMNH Mo167613. Arrow in 7 shows location of 6. Scale bars: 1-4, 7, 200  $\mu\text{m}$ ; 5, 100  $\mu\text{m}$ ; 6, 50  $\mu\text{m}$ .

depicted detail—by Cobbold (1934). Cobbold (1934) considered one specimen (possibly the one drawn by Salter, in Hicks 1872) to be the holotype. He also drew two additional specimens, revealing some variation in the sub-apical slope from slightly convex to moderately concave. Both Salter (in Hicks 1872) and Cobbold (1934) depict strong growth lines in these specimens, but Cobbold's drawing of the apparent holotype was more elongate than Salter's and had a curvature of the apical tip not seen in Salter's. However, because the type

specimens appear to have been lost, Runnegar (in Bengtson et al. 1990) designated the clearly similar species *Stenotheca acutacosta* Walcott, 1890 as the secondary standard for the genus. This species has the same degree of lateral compression, slight coiling, and prominent internal ridges as depicted in the drawings of *S. cornucopia*.

*Stenotheca?* from Landing and Bartowski (1996) has the lateral compression typical of stenothecids, but is fragmentary and lacks distinguishing features.



**FIGURE 14.** *Mellopegma indecorum* (Missarzhevsky in Rozanov et al., 1969) from the early Cambrian of Siberia. 1-6, SMNH Mo167615, locality indicated as middle Lena River, but without number; possibly M303/2), same specimen as in Missarzhevsky (1989; Plate VI, fig. 11), but with other side shown here. 5-6, detailed views showing possible traces of laminar shell microstructure. Arrows show possible imprints of crystal tablets. 7-9, SMNH Mo167616, locality 183e. 10-12, SMNH Mo167617, locality 183e. 13-16, SMNH Mo167618, locality M303/2. 17-20, SMNH Mo167619, locality M303/2. Scale bars 1-4, 10-14, 17-20, 200  $\mu$ m; 5-6, 5  $\mu$ m; 7-9, 15-16, 100  $\mu$ m.

**Range.** Early Cambrian (Botoman) to middle Cambrian.

**Occurrence.** United Kingdom (Wales), Canada (Newfoundland), China (Henan), and Australia (South Australia).

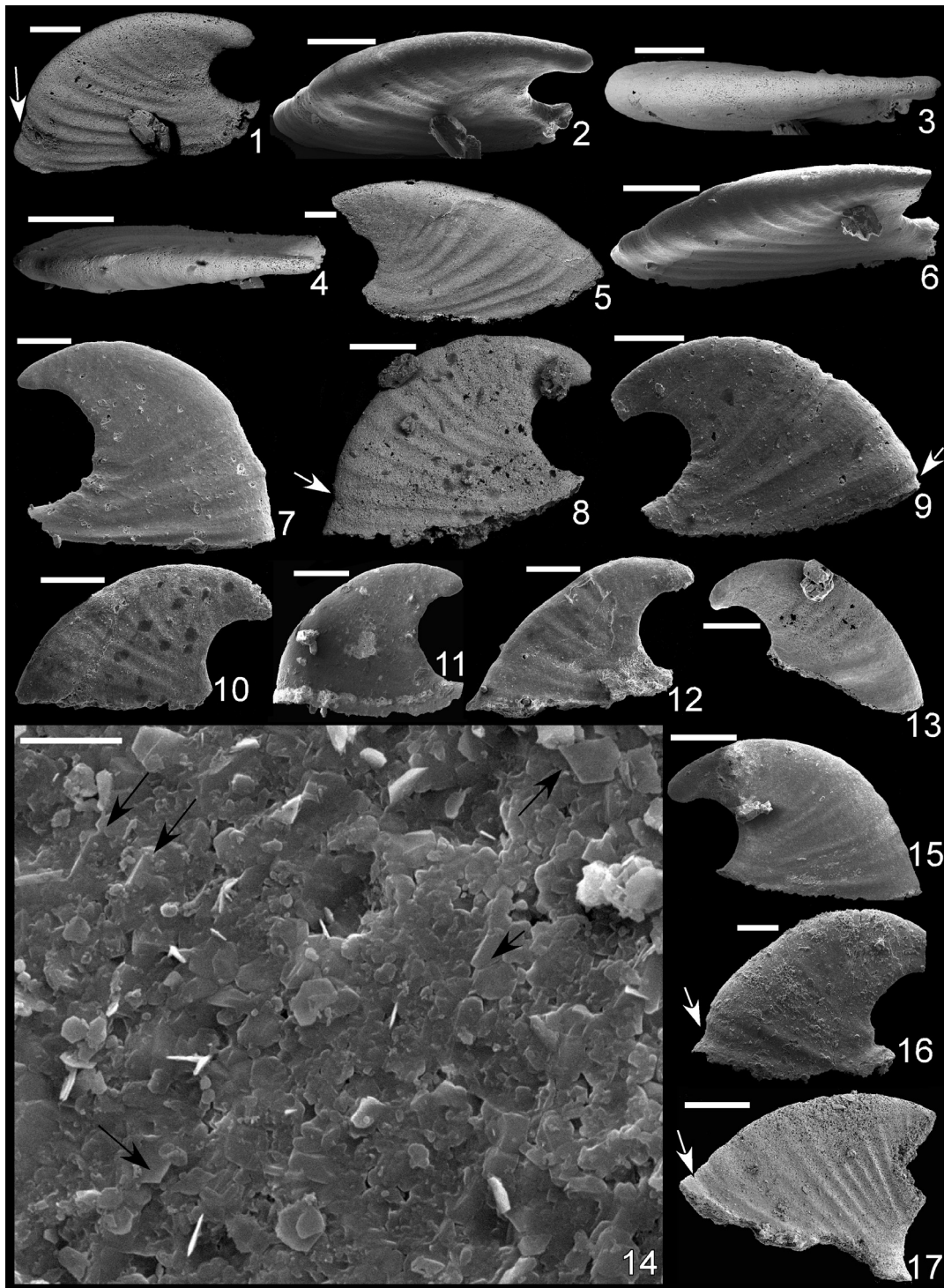
*Stenotheca drepanoida* (He and Pei in He et al., 1984)  
Figure 15

1984 *Anabarella drepanoida* He and Pei in He et al., 1984, p. 356, pl. ii, figs. 1-8.

1990 *Stenotheca* cf. *drepanoida*; Runnegar in Bengtson et al., p. 244, fig. 163b-g, m, n.

2001 *Stenotheca drepanoida*; Parkhaev in Gravestock et al., p. 183, pl. xlii, figs. 1-9.

**Material.** Twelve new specimens from the early Cambrian of Australia, UNEL localities L1852, 1874, and 1876 (Bengtson et al. 1990). One speci-



**FIGURE 15.** *Stenotheca drepanoidea* (He and Pei in He et al., 1984) from the early Cambrian of Australia (1-16), and *Stenotheca drepanoidea?* from the early Cambrian of Siberia (17). All specimens from L1876 (Bengtson et al. 1990) except 9, 11 and 16 (from L1852—Bengtson et al. 1990), 13 (from L1874—Bengtson et al. 1990), and 17 (locality 96-7/70; Botoman Stage; Kouchinsky 2000a). 1-3, holotype, SMNH Mo167620, early Cambrian of Australia, L1876 (Bengtson et al. 1990). 4-6, SMNH Mo167621, early Cambrian of Australia, L1876. 7, SMNH Mo167622. 8, SMNH Mo167623. 9, SMNH Mo167624. 10, SMNH Mo167625. 11, SMNH Mo167626. 12, SMNH Mo167627. 13, SMNH Mo167628. 14, SMNH Mo167629. Arrows show locations of imprints of crystal tablet faces. 15, SMNH Mo167630. 16, SMNH Mo167631. 17, SMNH Mo167632, early Cambrian of Siberia. All scale bars are 200  $\mu\text{m}$  except 5 with scale bar of 100  $\mu\text{m}$  and 14 with scale bar of 5  $\mu\text{m}$ .

men (Figure 15.17; SMNH Mo167632) from the early Cambrian of Siberia (sample 96-7/70, from the lower Botoman Stage of Siberia—Kouchinsky 2000a).

**Diagnosis.** Shell elongate, highly laterally compressed. Sharply concave sub-apical margin that terminates in a short sub-apical shelf. Internal and external ornament of comarginal rugae, less prominent on inner surface of shell. Typically a constriction on internal mould just above supra-apical margin. Apex curved a little more than 1/4 of a complete whorl, although some specimens show less coiling. High degree of variation in lateral profile.

**Description.** Shell elongate (c. 1.75 times longer than tall), laterally compressed (c. 5 times longer than wide); coiled less than half a whorl; dorsal margin strongly convex; margin under apex strongly concave; raised, narrow sub-apical shelf, curving slightly dorsally; tapered towards the sub-apical margin (Figure 15.3-4). Faint internal ridges become less prominent at anterior and posterior margins. Protoconch smooth, somewhat bulbous (Figure 15.2-3).

**Remarks.** In the original description of *Stenotheca drepanoida* (He and Pei in He et al. 1984) eight photographs were provided of multiple specimens, although a holotype was not designated. These specimens reveal significant variation in lateral profile in terms of degree of coiling, nearly grading in lateral profile into some specimens of *Anabarella australis* Runnegar (in Bengtson et al. 1990, fig. 163d-e). Only one of the specimens shown by He and Pei in He et al. (1984, pl. ii, fig. 3) is nearly as triangular in lateral profile as is the type species (based on illustrations) or the secondary standard species (based on photographs). Additional specimens that are somewhat intermediate between *A. australis* and *S. cornucopia*/*S. acuticostata* were referred to this species by Feng et al. (1994, pl. iii, figs. 3, 6, 7, 14, 15). Runnegar (in Bengtson et al., 1990) named a number of specimens from the early Cambrian of South Australia as *Stenotheca* cf. *drepanoida*. Parkhaev (in Gravestock et al. 2001) illustrated additional specimens from the same region and time period, classifying them as *Stenotheca drepanoida*. Clearly Runnegar's and Parkhaev's specimens and those herein described as *Stenotheca drepanoida* are members of the same species. Whether they are the same species as was shown in the original description of *Stenotheca drepanoida* is more speculative due to the wide variation in the latter, but some specimens

between these different sets are remarkably similar (e.g., compare He and Pei in He et al., 1984, pl. ii, fig. 3 with Figure 15.7 herein). Thus, it seems reasonable that all these specimens belong to *S. drepanoida*.

Runnegar (in Bengtson et al. 1990) noted that species such as *Mellopegma simesi* and *Stenotheca drepanoida* are difficult to classify. Much of the difficulty in classification of stenothecids, especially for *Stenotheca drepanoida*, is due to the remarkable intraspecific variation found in each bed. This variation makes classification difficult, but also reveals a striking degree of fuel for evolution in these stenothecid species.

*Stenotheca drepanoida* has less coiling and a more flared sub-apical margin compared with *Anabarella*. It has a greater degree of elongation and greater coiling than in *S. acuticostata* or *S. cornucopia*. *Stenotheca drepanoida* differs from *Mellopegma georginense* and *Mellopegma schizocheras* sp. nov. in having a more protruding, tubular apex and a less extensive sub-apical shelf; it differs from *Mellopegma simesi* comb. nov. and *Mellopegma uslonicum* in having a more smoothly rounded sub-apical margin; and from *Mellopegma indecorum* in being more laterally compressed.

**Range.** Early Cambrian.

**Occurrence.** Xinji Formation, Fangcheng County, Henan Province, China; and Mermerna Formation and Parara and Ajax Limestones, South Australia.

*Acanthotheca* gen. nov.

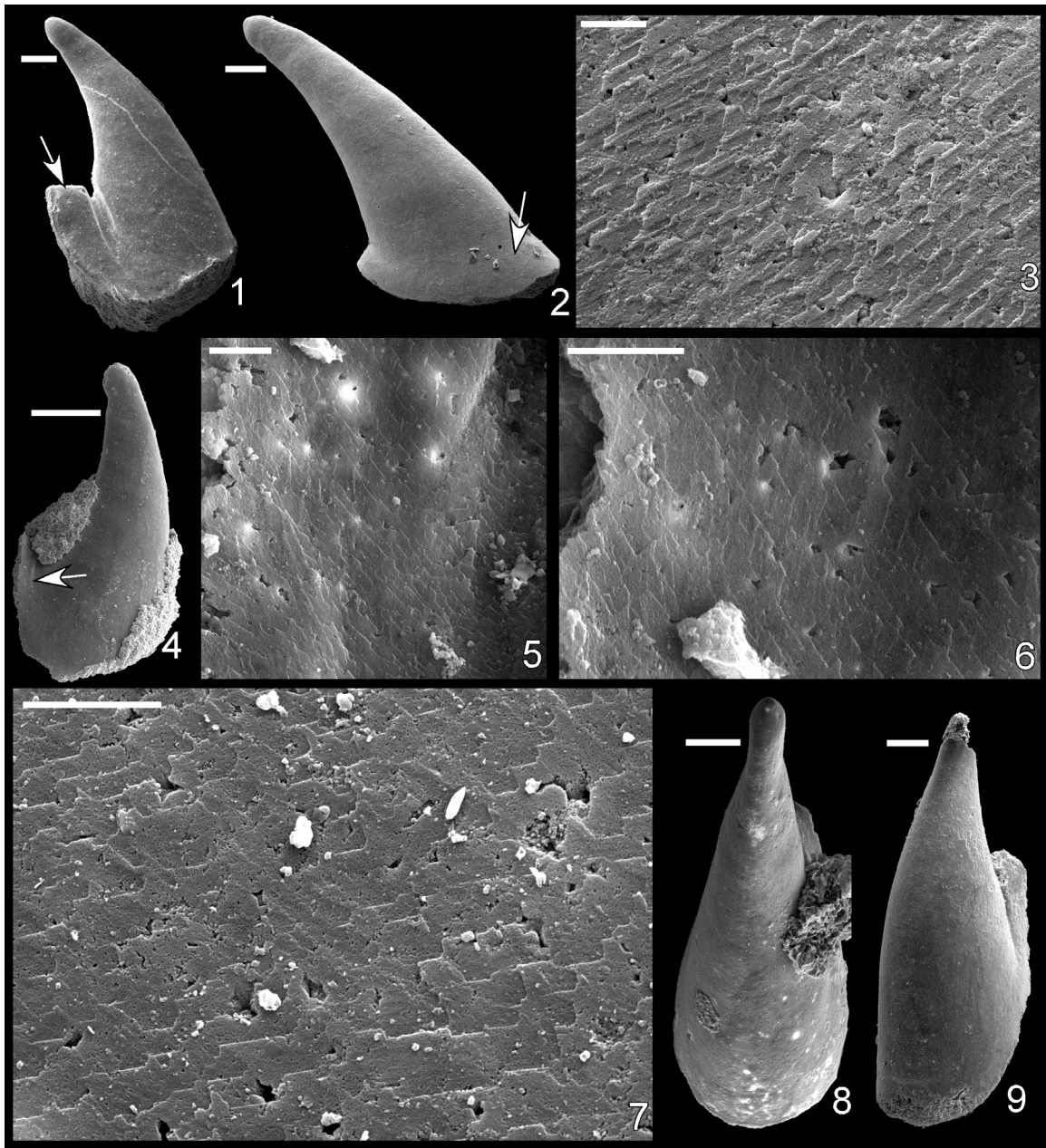
**Type species.** *Acanthotheca junior* (Runnegar, 1996), by monotypy.

**Etymology.** From the Greek *acanthos*, meaning thorn, and the Greek *theca*, meaning cup or container, with reference to the overall thorn shape of the shell ('cup').

**Diagnosis.** Shell small (c. 1 mm long), tall, sub-conical, slightly laterally compressed; ventral margin curved; sharp boundary in sub-apical slope at shelf.

**Remarks.** *Acanthotheca* shares key characters with other stenothecids, including a curved ventral margin, a gently curved dorsal margin, some lateral compression, and a laminar—possibly calcitic semi-nacre—inner shell layer. Although it lacks the same degree of lateral compression as most other stenothecids, its striking similarity in form to species such as *Mellopegma simesi* indicate it should be classified in the Stenothecidae. *Acanthotheca* differs from *Mellopegma* in having less lateral com-





**FIGURE 16.** *Acanthotheca junior* (Runnegar and Jell, 1976) gen. nov. 1, CPC 40508. Arrow shows imprint of pegma or pegma-like structure. 2, 3, CPC 39722. Arrow in 2 shows location of 3. 4-6, CPC 40509. Arrow in 4 shows location of 5 and 6. 7, CPC 39719. 8, CPC 39733. 9, CPC 39724. Scale bars 1-2, 8, 100  $\mu\text{m}$ ; 3, 5  $\mu\text{m}$ ; 4, 200  $\mu\text{m}$ ; 5-7, 10  $\mu\text{m}$ ; 9, 100  $\mu\text{m}$ .

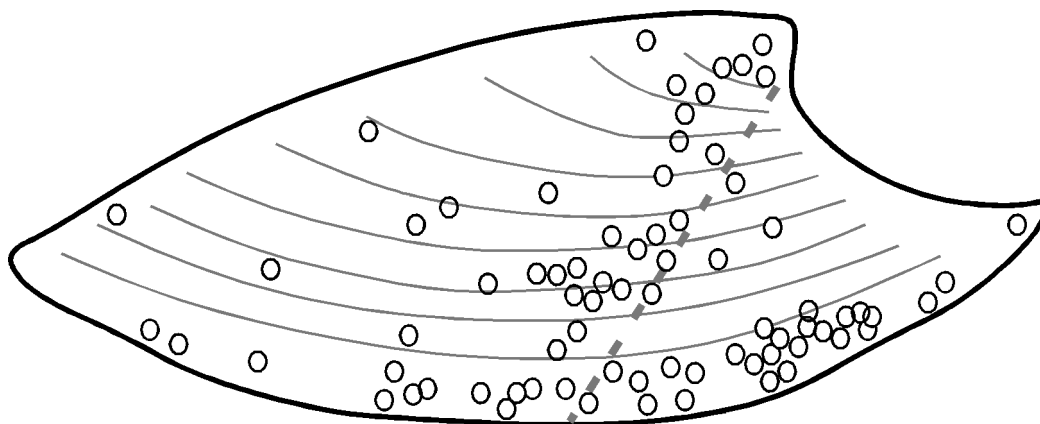
pression and a strongly developed pegma-like structure; it differs from *Stenotheca* in having less lateral compression, a greater degree of curvature of the ventral margin, and strongly developed pegma-like structure; it differs from *Anabarella* in coiling less than 1/2 a whorl; it differs from *Ribeiria* in coiling at all and in having a much more elongate apex, a less developed pegma, and greatest width in the supra-apical rather than sub-apical region.

**Range.** Middle Cambrian (Floran).

**Occurrence.** Only from Gowers Formation in the Thornton region of the Georgina Basin, Australia.

*Acanthotheca junior* (Runnegar, 1996)  
Figure 16

1996 *Ribeiria junior* Runnegar, p. 85, fig. 6.2k.



**FIGURE 17.** Centres of damage on fifty-two shells of *Mellopegma georginense* Runnegar and Jell, 1976 and *Mellopegma schizocheras* sp. nov. from the Gowers Formation. Damage inferred on internal moulds from imprints of scars and embayed regions of missing shell, usually with smooth margin of damaged area. Note the concentration of damage in the sub-apical region of the shell. Dashed line shows location of zygion in the related species *Eurekapegma cooperi* MacKinnon, 1985.

2010 *Ribeiria junior*; Vendrasco, Porter, Kouchinsky, Li, and Fernandez, p. 130, pl. 3.

**Diagnosis.** As for genus.

**Remarks.** Runnegar (1996) classified this species as a member of *Ribeiria* based on the overall shape and apparent pegma in the one known specimen at the time. Vendrasco et al. (2010) illustrated many more specimens that reveal the pegma-like structure is variously developed in different individuals. In addition, this species differs from members of *Ribeiria* Sharpe, 1853 in being taller/less elongate, having a shell with at least some coiling (~1/4 whorl), and having the greatest width in the supra-apical rather than sub-apical region of the shell. *Acanthotheca junior* may be ancestral to *Ribeiria*.

**Range and Occurrence.** As for genus.

## DISCUSSION

Here we discuss the relevance of the new data on *Mellopegma* and other stenotheccids to the following topics: functional morphology; escalation with predators; phylogeny; and shell characteristics including microstructure, the presence of pores, and the periostracum.

### Shell Damage and Cambrian Escalation between Molluscs and Their Predators

Numerous specimens of the most abundant species of *Mellopegma*, *M. georginense* and *M. schizocheras* sp. nov., show imprints of shell scars, typically expressed as indentations on the internal

moulds (Figures 6.4, 6.10-11, 6.14, 9.5, 9.10-12). Several specimens also show missing regions of shell, often with a smooth margin (Figure 8.18-21). The smooth borders around most signs of damage, both scars and missing pieces, suggest that many breaks were healed during the lifetime of the animals. While it is difficult to rule out a mechanical cause of this damage, several lines of evidence support predation as a cause of most of the wounds: (1) the attacks occur at a higher frequency in the sub-apical region (Figure 17), the area with the largest aperture width and hence easiest access to the animal's flesh; (2) in many cases the wound tapers upward (Figure 6.4, 8.18, 9.5, 9.10-11), a pattern that would be produced by the tip of an appendage, versus mechanical damage which would produce more variation in form; (3) specimens interpreted as coprolites that contain bradoriid shells occur in these beds (Figure 7.12), revealing the presence of a predator on small animals; and (4) the many other signs of predatory activity in Cambrian fossils (see below). It must be kept in mind, though, that such a potential shell-breaking predator of *Mellopegma* must have been small, as *Mellopegma* was on the order of a millimetre long.

*Mellopegma* was a tiny burrowing animal and so may have escaped the senses of larger predators, but Swedmark (1968) pointed out that modern interstitial organisms even in subtidal environments need mechanical protection from damage caused by shifting sediment and smaller predators. Although the shell of *Mellopegma* is revealed in thin sections to have been quite thin (c. 10-20  $\mu\text{m}$

total shell thickness; Figure 7.1-4), the organic-rich shell with a laminar inner layer may have helped it resist some attacks (see below). Moreover, the highly organic prismatic shell layer in *M. georginense* probably provided additional flexibility to the shell that helped prevent shell fracture during attack.

Clear evidence of predation is well-known from the Cambrian, including bite marks, healed scars, drill holes, and predatory appendages (e.g., Alpert and Moore 1975; Miller and Sundberg 1984; Jensen 1990; Conway Morris and Bengtson 1994; Skinner 2005; Vannier and Chen 2005) and in fact traces of predation have been described in fossils as old as the Late Precambrian (Bengtson and Zhao 1992; Hua et al. 2003). It is clear that large predators such as *Anomalocaris* roamed Middle Cambrian seas (Whittington and Briggs 1985), although smaller predators are also known. For example, the priapulid *Ottoia* ranged from 2-16 cm (Briggs et al. 1994) and has been found with hyolith and other shells in its gut; in these cases though the hyoliths are about four times the length of a typical specimen of *Mellopegma*. The strongest evidence for predation being a powerful selective factor at small sizes during the Cambrian comes from traces such as boreholes in small fossils (e.g. Bengtson and Zhao 1992, Conway Morris 1998). However, fossils of predators in the same rocks that preserve *Mellopegma* have not been found.

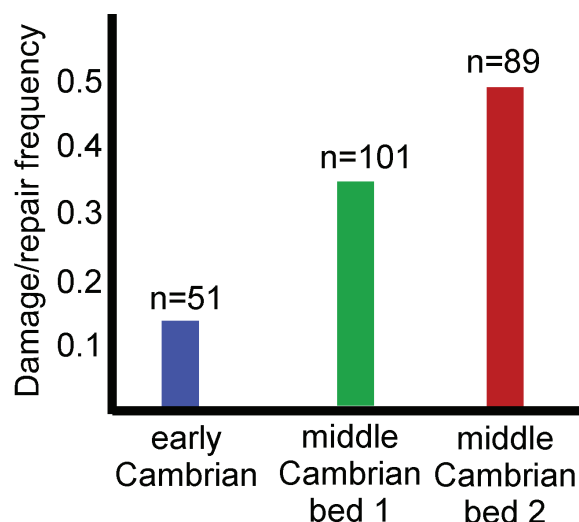
In modern molluscs predation is the predominant cause of shell damage, with molluscs in turbulent waters without predators suffering much lower rates of shell injury than molluscs in calm waters with predators (Vermeij 1987). Shell damage from predatory attack has been well documented in Paleozoic brachiopods (Alexander 1986) and molluscs (Schindel et al. 1982; Peel 1984; Lindström and Peel 1997, 2003). Skovsted et al. (2007) demonstrated shell repair in an early Cambrian mollusc deposited in a low energy environment, concluding that predation must have caused the injuries. In addition there is a high frequency of angular fragments of fossils in the Gowers Formation assemblage, and such fragments are typically produced by durophagous predation rather than physical factors (Oji et al. 2003).

Specimens of *Mellopegma georginense* show a relatively high frequency of healed damage (Figures 5.7, 6.4, 6.10-11, 6.14, 9.1, 9.5, 9.10-12), possible bite marks (Figure 8.18-21), and fragmentation. Although the apparent bite marks and fragmentation may have been caused by

taphonomic factors, the healed injuries clearly occurred during the life of the animal. Although shell crushers in the early Paleozoic were relatively inefficient (Vermeij 1987), predators with the capability to damage the thin shells of early molluscs like *Mellopegma* likely existed in the early Cambrian (Skovsted et al. 2007).

The shell of *Mellopegma* was especially thin, but its innermost shell layer consisted of calcitic semi-nacre, which is very similar in form to aragonitic nacre (Weedon and Taylor 1995), a very strong microstructure (Currey 1977; Jackson et al. 1988, 1990). Nacre is thought to be energetically costly and time consuming to produce, largely because of its high organic component (Currey 1977). It is unclear to what extent the calcitic semi-nacre in *Mellopegma* had similar costs and benefits to aragonitic nacre, but *Mellopegma* had a flexible outer prismatic shell layer that would have helped it withstand shell-crushing predators. *Mellopegma* also possessed many of the other defensive traits against shell-crushing predators that were described by Vermeij (1987), including several characters that would have assisted in escape via vertical burrowing (Table 2).

Most of the healed marks on *Mellopegma* occur along the ventral margin (Figures 6.10, 8.18-21, 9.1, 9.10-11), and usually the damage was centered on the apical half and near the aperture (Figure 17). These observations suggest that the ventral margin, and likely the sub-apical side, of *Mellopegma* was exposed above the sediment surface, lending support to Runnegar's (1996) and Peel's (1991b) interpretation of the life position of the similar *Eurekapegma*. The main difference between *Mellopegma* and *Eurekapegma* is the presence in the latter of an internal plate called the zygon (MacKinnon, 1985). This plate extended from the apex to the ventral margin in the area where most of the healed damage in *Mellopegma* occurred. It, therefore, seems likely that at least one function of the zygon of *Eurekapegma*, an inferred descendent of *Mellopegma* (MacKinnon 1985; Peel 1991b; Runnegar 1996), was to support the shell in resisting crushing forces of predators. The zygon, a relatively thick internal plate that extended from one side of the shell to the other, would have resisted perpendicular lateral crushing forces at the easiest region of the shell to clamp. Moreover, a long region of the ventral margin on the apical side of *Eurekapegma* is sealed by a convergence of the two sides of the shell (MacKinnon 1985, fig. 3l,m,s,v), providing more evidence that



**FIGURE 18.** Proportions of stenothecids with damage from the early Cambrian Parara Limestone of Australia (including *Anabarella australis* and *Stenotheca drepanoidea*) and from two different beds of the middle Cambrian Gowers Formation of Australia (including *Mellopegma georginense* and *Mellopegma schizocheras*). Bed 2 is stratigraphically above bed 1.

this was a vulnerable area in its immediate ancestors.

Preliminary analyses of damage frequency provide some additional evidence in support of escalation between micromolluscs and predators over different time scales in the Cambrian (Figure 18). Proportions of damage in stenothecids were compared between the early Cambrian Parara Limestone and the middle Cambrian Gowers Formation, and also between two beds within the Gowers Formation. The damage rate of specimens from the Parara Limestone was 0.137 ( $n=51$ ). The damage rate of specimens from the lower bed in the Gowers Formation was 0.347 ( $n=101$ ) and from the upper bed 0.494 ( $n=89$ ). The z-value for the difference between the early Cambrian versus the lower of the two middle Cambrian beds is 2.531 (99.4% confidence level); the z-value for the difference between lower and upper of the middle Cambrian beds is 1.917 (97.2% confidence level). Thus the results of this preliminary study of damage proportions in stenothecids through the Cambrian are consistent with escalation in predation intensity, although additional beds should be studied to confirm this pattern.

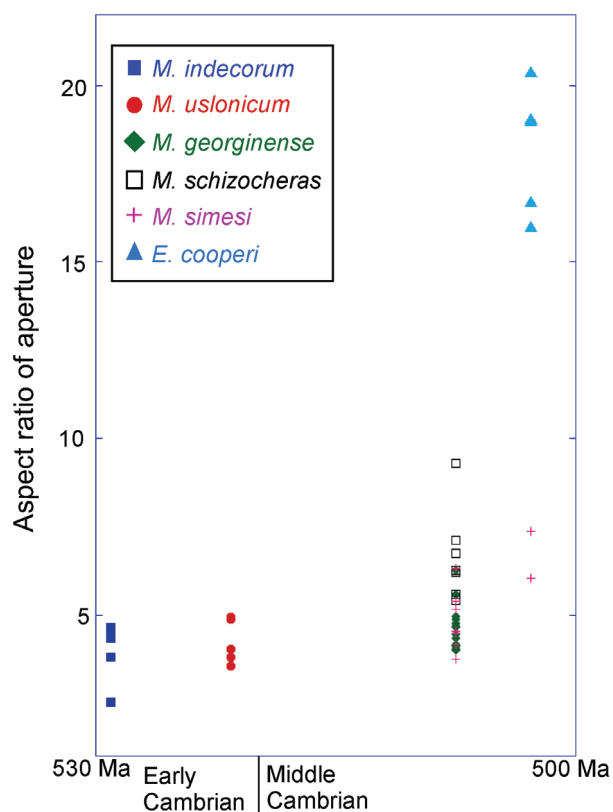
At the small sizes and miniscule shell thicknesses that characterize stenothecids, it is difficult to estimate the full range of predation pressure. Perhaps predation was just as high in the early Cambrian as in the middle Cambrian, but shell

strength was lower then and shells may have often been totally demolished (and thus not preserved). In any case the frequency of damage caused by small shell-crushing predators that were not able to obliterate the thin, small shell of stenothecids increased through this time period, and other morphological trends in this family indicate increasing defense. For example, the *Mellopegma* lineage shows a trend toward increasing narrowness of the aperture (Figure 19), a defensive characteristic (Vermeij 1987) with high expense as it severely limits the space for organs inside the shell. This narrowing reached its zenith in the youngest form, *Eurekapegma cooperi*. Apertural narrowing would allow for faster burrowing to escape predators, and it would have made it more difficult for predatory appendages to reach into the shell. Thus the combined evidence indicates that *Mellopegma* was involved in a Cambrian arms race between small predatory arthropods or worms and tiny shelled molluscs.

### Shell Characteristics

The phosphatic moulds reveal new details about the shell morphology of *Mellopegma*, including the form and organization of the outer prismatic and inner laminar (calcitic semi-nacre or similar) shell layers, the nature of the shell pore system, the form of the periostracum, and the shape and size of the protoconch.

**Shell microstructure.** Preservation of shell microstructure in *Mellopegma* has been known for many years. Runnegar (1985) described polygonal imprints near the aperture margin and angular imprints elsewhere in *Mellopegma georginense*, and suggested this species had nacreous inner and prismatic outer shell layers. New data presented here and in Vendrasco et al. (2010, table 2) confirm the presence of an inner laminar layer and an outer prismatic layer. However, the results of our comparisons of many aspects of the fossil imprints – including interfacial angles – with the variation in modern shell microstructures largely support the hypothesis that the inner shell layer was calcitic semi-nacre instead of (aragonitic) nacre (Vendrasco et al. 2010). In addition, studies here suggest that (1) *Mellopegma* had an inner shell layer composed of calcitic semi-nacre (the calcitic version of the shell microstructure defined by Carter et al. 1990, p. 611, as “laminae consisting of polygonal tablets which show more abundant screw dislocations and less lateral continuity of the laminae than in typical nacreous structure”) that was highly organized and consisted of many



**FIGURE 19.** Aspect ratio of aperture of *Mellopegma* and *Eurekapegma* through time. Aspect ratio measured by dividing the length of aperture by the average of its maximal and minimal width.

stacks of laminae; and (2) *Mellopegma* had a prismatic outer shell layer that varied widely in form and region of exposure on the inner shell surface (where the inner shell layer was thin or missing) between the three species from the Gowes Formation – *M. georginense*, *M. simesi*, and *M. schizocheras* sp. nov. The type of calcitic semi-nacre expressed in Craniiformean brachiopod shells is high magnesian (Cusack et al. 2008), which probably also characterized the inner shell layer of *Mellopegma*, in accordance with the Tommotian transition to calcite seas.

Internal moulds of *Mellopegma georginense*, *Mellopegma schizocheras* sp. nov., *Mellopegma simesi* comb. nov., *Mellopegma uslonicum*, and *Mellopegma?* illustrated herein show imprints of shell microstructure. Specimens of *Mellopegma indecorum* that we examined have less distinct imprints of shell microstructure, but the limited evidence suggests a microstructure consistent with that found in the other species of *Mellopegma*.

New data presented here reveal more details about the outer prismatic shell layer and its varia-

tion among *Mellopegma* species. For example, *M. georginense* and *M. schizocheras* sp. nov. differ significantly in the form of the polygonal organic framework of prismatic microstructure and the distribution of imprints of this texture over the surface of internal moulds. In *M. georginense* the polygons are small (a few  $\mu\text{m}$  diameter), thick-walled, and occur over most of the surface of the internal mould, except at or near the apex (Figures 5.13, 5.16, 5.22, 6.12-13, 6.15). In *M. schizocheras* the polygons are large (about 20  $\mu\text{m}$  diameter), thin-walled, and occur only at the sub-apical and to a lesser extent the supra-apical regions of the aperture margin (Figure 9.3-4, 9.7). This disparity in polygon size, form, and distribution between *M. georginense* and *M. schizocheras* sp. nov. represents a major difference between these two similar taxa.

The polygonal network in the case of *M. schizocheras* sp. nov. is clearly an imprint of prismatic shell microstructure, as its pattern is very similar to that in epoxy moulds made of prismatic microstructure in modern molluscs (Vendrasco et al. 2010, pl. 10, figs. 1-4), and it occurs near the aperture of the internal mould, where the addressed shell typically thins out and expresses the outer shell microstructure on the inner shell surface. The polygons in *M. schizocheras* sp. nov. might be the infill of prisms whose organic walls decayed away (*sensu* Kouchinsky 1999), or may represent an active replacement of the organic conchioloin walls (*sensu* Vendrasco et al. 2010).

In specimens of *M. georginense* the polygonal texture looks different from the polygonal texture in *M. schizocheras* and many other Cambrian molluscs, and instead looks similar to pores on the external surface of some molluscs such as chitons. This observation indicates the possibility that the polygonal texture in *M. georginense* might instead be external ornament, and that these specimens are shell replacements or casts instead of internal moulds. However, evidence that this texture is an imprint of inner shell microstructure and not external ornament includes the observations that: (1) imprints of calcitic semi-nacre tablets – a clear indicator of shell interior – overlie the polygonal network (Figure 6.12-13, 6.15); (2) the polygonal network is visible on every specimen in an assemblage heavily dominated by internal moulds; and (3) tubercles similar to those on internal moulds of other taxa, which represent the cast of internal shell tunnels (Kouchinsky 2000a; Parkhaev 2006; see below), occur within the polygonal network (Figure 5.16).



The polygonal network in *M. georginense* is perplexing in that it occurs over most of the surface of the internal mould, except at or near the apex, instead of just at the aperture margin. The polygonal network has the overall appearance of an organic matrix, which is common in all shells of molluscs and helps control crystal deposition in shell formation. The polygonal network is interpreted here as an imprint of an outer prismatic shell layer, in which case the inner laminar calcitic semi-nacre shell layer must have been very thin so that on internal moulds its imprints would not fully cover the prismatic layer. If this interpretation is correct, the prismatic shell layer consisted of small crystals embedded in a thick, flexible conchiolin matrix. Alternatively, this organic matrix perhaps was not part of a prismatic shell layer but instead seeded the incipient crystals of calcitic semi-nacre. Imprints of calcitic semi-nacre occur over the polygonal network (Figure 6.12-13, 6.15), and so clearly this organic layer was either part of that inner laminar shell layer or it occurred right at the boundary between the outer prismatic and inner laminar shell layers.

Distinct traces of prismatic shell microstructure have not been observed in specimens of *Mellopegma simesi* comb. nov. or in the early Cambrian *Stenotheca drepanoidea* or *Mellopegma indecorum*. *M. simesi* is known from many specimens with well-preserved laminar shell microstructure, so the lack of polygonal texture in this species is perplexing. Perhaps the shell of *M. simesi* did not thin out as much distally as in other species of *Mellopegma*, and so the outer prismatic shell layer would only be seen in the inner shell surface if it were significantly abraded. Although the few known specimens of *Mellopegma uslonicum* lack well-preserved polygons, tubercles are prominent (Figure 12.6) and in some cases (Figure 13.6) the tubercles are linked up in a way reminiscent of the faintly preserved polygons of *M. schizocheras* sp. nov. (Figure 9.3-4, 9.6-7). Such faint merging of tubercles is seen to a lesser extent in *M. simesi* (Figure 11.1), but is less convincing a reflection of prismatic microstructure than is the comparable texture in *M. uslonicum*.

The new fossils of *Mellopegma* also reveal additional information about the inner laminar shell microstructure in members of this genus. All species of *Mellopegma* have a laminar inner shell layer. In *M. georginense* and *M. simesi*, the laminar microstructure is calcitic semi-nacre (Vendrasco et al. 2010). Based on the overall similarity in tablet imprints with these species, the other species of

*Mellopegma* probably had an inner shell layer of calcitic semi-nacre as well.

The imprints of laminar microstructure in *Mellopegma* show that the crystal tablets in the inner shell layer were highly organized, with consistent orientation of the crystals within the layer (Figure 9.8-9, 11.5-9). This structure suggests that Cambrian molluscs had a precise ability to control the microstructure of their shell, and that crystal nucleation was strongly guided, most likely by an organic matrix. This high degree of organization of the inner laminar layer also characterizes modern bivalve sheet nacre (compared with the less organized gastropod columnar nacre) (Taylor et al. 1969), providing support for a close relationship between *Mellopegma* and bivalves.

The fossils also reveal that each lamina was quite thin, as suggested by the imprints of tablets on multiple vertical levels (Figure 11.7) and the observations of replaced sheet-like laminae overlying the internal mould surface in some specimens (Figures 5.17, 6.8, 6.14, 9.8-9, 11.7). There also appears to have been a tall stack of many laminae of calcitic semi-nacre that made up the inner shell layer of *M. schizocheras* sp. nov. and *M. simesi* (Vendrasco et al. 2010, pl. 1, fig.10, pl. 2, figs. 9-10, 12).

The occurrence of a laminar microstructure in *Mellopegma uslonicum* (Figure 12.5-9) similar to the calcitic semi-nacre in *M. georginense*, *M. simesi*, and *M. schizocheras* adds to the evidence that it is closely related to other *Mellopegma* species and extends back the history of this unusual type of laminar shell microstructure to the early Cambrian. Faint traces of a similar laminar shell microstructure made up of angular tablets can be seen in the other early Cambrian stenothecids as well (*Mellopegma indecorum* (Figure 14.5-6) and *Stenotheca drepanoidea* (Figure 15.14)), although the preservation in these cases is too poor to allow a detailed comparison with other species of *Mellopegma*. *Acanthotheca junior* (Figure 16.3, 5-7) also shows distinct laminar microstructure that appears to be calcitic semi-nacre, strengthening the link between this taxon and *Mellopegma*. Calcitic semi-nacre thus characterizes *Mellopegma* and perhaps the Stenothecidae overall.

Calcitic semi-nacre is also known in platyceratoid gastropods from the Paleozoic (Carter and Hall 1990) but is otherwise rare in the Mollusca. Calcitic semi-nacre is more common in brachiopods (Williams and Wright 1970) and bryozoans (Weedon and Taylor 1995), and its occurrence in molluscs reveals a fundamental similarity in biom-

neralization between these lophotrochozoan taxa. The new data here show that calcitic semi-nacre dates back at least to the early Cambrian in molluscs, providing more evidence that it may have been a primitive shell microstructure in both molluscs and calcitic brachiopods. Similarity in shell formation between brachiopod and early molluscan shells was noted by Carter (1979), who suggested both groups had shell microstructure where the component crystals are not uniformly oriented in three dimensions (vertically and horizontally). This ancestral mode of biomineralization became more extensively modified in later molluscs than in brachiopods (Carter 1980). Molluscs and brachiopods are in the same major clade of Lophotrochozoa (Dunn et al. 2008, fig. 1, clade C), but the many soft-bodied taxa in this clade (i.e., molluscs and brachiopods each have soft-bodied taxa as their close relatives) make it unreasonable to assume that a shell was primitive in this clade. However, it is possible that the most recent common ancestor of brachiopods and molluscs had similar organic precursors in shell formation, leading to similar shell microstructures in their early history. In spite of the differences between modern mollusc and brachiopod shells (e.g., some brachiopod shells are phosphatic whereas no mollusc shells are; calcareous brachiopods are calcitic whereas molluscs are more often aragonitic; and molluscs have a greater diversity of shell microstructures), there are many similarities, including: (1) extensive shell pore system seen in chitons and many early Cambrian molluscs – see “Shell pores” below; (2) organic-rich shell; (3) mantle; (4) periostracum; (5) a complex shell with different types of shell microstructure in different layers; and (6) similar types of shell microstructure (all types of brachiopod shell microstructure are also seen in molluscs – Carter and Clark 1985).

Many different lineages of animal appear to have independently evolved a shell over the geologically short “Cambrian explosion” (Bengtson and Conway Morris 1992), suggesting that the evolutionary precursors to shell formation occurred in these taxa. Evidence for underlying homology in the shells of metazoans has been provided by Jacobs et al. (2000), who demonstrated that *engrailed* expression is involved in skeletal formation in a wide range of bilaterians. There was probably a high degree of homology in the precursors to shell formation in molluscs and brachiopods, explaining the great number of similarities in the shell and its formation between these taxa. The common ancestor of these taxa likely had a similar

organic coat and genetic framework for constructing a shell. The occurrence of calcitic semi-nacre in molluscs from the early Cambrian described here reveals a stronger homology in shell formation among molluscs and brachiopods than previously realized.

**Shell pores.** *Mellopegma* is characterized by a pore system that extended through much or all of the thickness of the shell, connecting with the conchiolin of the prism sheaths in the outer prismatic shell layer. Kouchinsky (2000a) had previously noted the occurrence of “tubercles” or small protrusions on the surface of internal moulds of many early molluscs. He interpreted these structures as in-filling of pores on the inner surface of the shell. Feng and Sun (2006) and Parkhaev (2006) described numerous additional observations of pores in early molluscs, revealing that many early Cambrian molluscs had pores that infiltrated the shell, in some cases extending through the entire shell thickness (Parkhaev 2006, fig. 3). The evidence for pores consists of casts of the entire vertical canals extending from the surface of internal moulds, and, more commonly, tubercles, interpreted as partially broken casts.

The surface of internal moulds of *Mellopegma uslonicum* contains large-diameter (~ 3–4  $\mu\text{m}$ ), conical tubercles with a blunt end, suggesting that this species had relatively large shell pores that either ended abruptly or, more likely, were incompletely preserved (Figure 12.4; Parkhaev 2006). Runnegar and Jell (1976; fig. 8b8) noted tubercles on the internal molds of *Mellopegma georginense* and concluded this species had depressions on the internal surface of the shell. These depressions are interpreted here as a shell pore system, or a remnant of one that was more extensive in the early representatives of *Mellopegma*.

Many of the new specimens of *M. georginense*, *M. schizocheras*, and *M. simesi* have tubercles on the surface of the internal mold, sometimes merged together (Figures 5.15–16, 9.6), and in many cases clearly in line with growth lines (Figure 5.15). These tubercles are typically best preserved at the apex (Figure 5.8) and along the dorsal ridge (Figures 5.9, 10.17, 11.1). At the anterior and posterior margins of *M. schizocheras* sp. nov., such tubercles can be seen at polygon boundaries (Figure 9.3–4, 9.6) and so pores may have occurred in between prisms of the outer shell layer. The pores in *Mellopegma*, best seen in *M. uslonicum*, are smooth-walled (Figure 11.4), which suggests they may have had an inner lining of – or were entirely filled with – tissue.

Some specimens of *M. georginense* and *M. schizocheras* appear to show that the organic sheaths around the prisms of the outer prismatic shell layer were in contact with the vertical pores (Figures 5.16, 9.3-4, 9.6-7). This configuration makes it clear that the pores extended through most or all of the thickness of the shell, as they open at the inner surface of the shell (bumps over much of surface in internal moulds) and extend above the base of the outer prismatic shell layer (bumps at nodes of polygons near aperture where outer prismatic shell layer is preserved). However, the function of this pore system in *Mellopegma* and the significance of a connection to the conchiolin sheaths are at present unclear.

Shell pores occur in many modern molluscs. They are extensively developed in chitons, including the earliest known representatives (Pojeta et al. 2010), and also occur in gastropods (Reindl and Haszprunar 1996), the Palaeozoic monoplacophoran *Tryblidium* (Erben et al. 1968), and in many bivalve superfamilies where they penetrate the entire shell (Taylor et al. 1969). The pores in *Mellopegma* are most similar to those in bivalves; as with bivalve tubules, those in *Mellopegma* are inferred to have possessed a smooth surface and a cylindrical shape, and to have extended through much or all of the shell.

The current list of early Cambrian molluscs with evidence of shell pores is provided in Appendix 2. It appears that shell pores were either primitive in the Mollusca or that pores independently and rapidly evolved in different early Cambrian lineages (note in particular the occurrence of pores in the possible gastropods *Barskovia* and *Philoxenella* as well as diverse groups of helcionellids). Evidence in support of the hypothesis that shell pores in molluscs are primitive include: (1) the occurrence of shell pores among representatives of many groups of modern molluscs (Reindl and Haszprunar 1996); (2) their prevalence among early Cambrian molluscs (Parkhaev 2006); (3) their prominence in lophotrochozoans closely related to molluscs, including brachiopods (Reindl and Haszprunar 1996) and sipunculans (Ruppert and Rice 1995); and (4) their prevalence in other taxa thought to be molluscs or closely related to them, such as hyoliths (Kouchinsky 2000b) and coeloscleritophorans (Bengtson 1992) like halkieriids (Vinther 2009). Although some of these pore systems in various modern molluscs appear structurally different and so perhaps are not homologous (Reindl and Haszprunar 1996), their widespread occurrence in the earliest known molluscs and

other evidence listed above suggests pores may be primitive in this phylum, and were subsequently lost in major branches of molluscs. Pores are probably even more widespread among Cambrian molluscs than the data currently suggest because: (1) pores might not have been common or large in some shells and so were not commonly fossilized; (2) some pore openings may not have been filled by the phosphate that coated the shell (evidence for this can be seen in the variable preservation of pores in single specimens); (3) some Cambrian species are not known from well-preserved specimens such as fine-grained internal moulds; and (4) in some cases pore fillings might not have been noted in descriptions and cannot be identified in pictures from the literature.

**Periostracum.** One specimen of *Mellopegma georginense* shows prominent radiating ridges over the surface of an apparent cast (Figure 5.18-19). These ridges originate at the apex and curve downwards to the aperture. Similar structures can be seen in other middle Cambrian molluscs, including *Pseudomyona queenslandica* (Gubanov et al. 2004, fig. 9g-h), *Yochelcionella ostentata* (Gubanov et al. 2004, fig. 6s), and *Anabaroconus sibiricus* (Gubanov et al. 2004, fig. 5n). Gubanov et al. (2004) did not provide an interpretation of these structures, but we interpret them to be a replacement of a portion of the periostracum layer. The periostracum is the outermost, entirely organic, layer of the molluscan shell that in modern forms consists mostly of quinone-tanned proteins. We interpret the fossil structures to be replaced periostracum because: (1) in each case the structure covers all other textures on the fossils, consistent with it being the external periostracum layer; (2) it is rarely preserved (seen in only one specimen of *Mellopegma* out of more than 100 examined via SEM), consistent with being an organic structure that degraded quickly after the animal's death, and inconsistent with being external ornament; (3) the radial ridges extend the full height of the shell (from apex to aperture), consistent with an organic covering but inconsistent with shell microstructure; and (4) on specimens where it is preserved there is variation in prominence of ridges from one region of the shell to the next, and often it is only faintly preserved in spite of consisting of thick ridges. The last point is consistent with the hypothesis that this structure is a replacement of an organic layer and inconsistent with the hypothesis that it represents external shell ornament; a thick-ridged external ornament should be more conspicuous and evenly preserved in the fossils.

The periostracum aids in the initial formation of the shell, in isolating the mantle cavity from the surrounding seawater, and in protection (Taylor et al. 1969). Its importance plus its widespread occurrence in conchiferans and chitons suggest that this layer originated early in the evolution of shelled molluscs. The findings in Gubanov et al. (2004) and herein provide direct evidence for this hypothesis, revealing that Cambrian molluscs had a thick periostracum. These observations suggest that the mechanism of biomineralization that characterizes modern molluscs was already in place during the Cambrian, a mechanism wherein the chemistry in the mantle cavity – isolated from the external environment by the periostracum – is controlled to induce crystal initiation and growth.

**Protoconch.** The protoconch is obvious in most well-preserved specimens of *Mellopegma*. It is a simple cone whose internal mould is smooth with scattered tubercles (e.g., Figures 5.8, 6.7). The protoconch in *Mellopegma* is typically ~150-200 µm in length, in line with the range in modern monoplacophorans (Marshall 2006). The large size of protoconch 1 (the initial part of the protoconch, formed inside the egg capsule) suggests lecithotrophic development. Bivalves with lecithotrophic development tend to have a small or non-existent Prodissoconch 2 (Jablonski 1985), which might explain why this boundary is not readily identifiable in *Mellopegma*. Similarly, the early Cambrian bivalve *Pojetaia runnegari* had only a large (~150 µm), single prodissoconch (Runnegar 2007).

Nützel et al. (2006) suggested that Cambrian molluscs had lecithotrophic larvae and that planktotrophic larvae evolved in the Ordovician. Freeman and Lundelius (2007) instead argued that planktotrophy was primitive in molluscs. Both teams used as evidence measurements of Cambrian fossils, mostly phosphatic internal moulds. Runnegar (2007) criticized the validity of these measurements but noted that the few clear cases of protoconchs in Cambrian molluscs suggest they were lecithotrophic. *Mellopegma* provides another example of a Cambrian mollusc with a clear, large protoconch suggestive of non-planktotrophic larvae.

Martí Mus et al. (2008) provided fossil evidence that some helcionellids were juvenile shells of much larger animals with broader, limpet-like shells. Extrapolating this idea to a large fraction of helcionellids is problematic, however. In the case of *Mellopegma*, the distinct larval shell, consistent size range of specimens, lack of larger calcitic specimens in the rocks, and unbroken ventral mar-

gin in many specimens all indicate that it is the adult shell that is preserved.

### Functional Morphology of *Mellopegma*

The laterally compressed shell suggests that *Mellopegma* was at least semi-infaunal, or – given its small size – interstitial. The life position of *Eurekapegma* MacKinnon, 1985, which had a very similar shell to *Mellopegma*, has been debated. MacKinnon (1985, figure 6a) postulated that the internal plate (zygion) of *Eurekapegma* provided an area for attachment of muscles from the foot and that the sub-apical region of the shell was buried in sediment. Peel (1991b) reversed this orientation, postulating that in *Eurekapegma* the supra-apical surface was buried, and that the zygion delimited the posterior mantle cavity with gills to the sub-apical region exposed above the sediment. Runnegar (1996) agreed with Peel that the supra-apical surface was buried, but disagreed with Peel's (1991b) assertion that it was the posterior of the animal that was exposed. Runnegar (1996) also noted that at these small sizes drawing water into and through the body would have been comparable to honey sucked through a straw. Either *Mellopegma* did not actively draw in water, or it spent significant metabolic energy to do so.

Many specimens of *Mellopegma georginense* and *Mellopegma schizocheras* sp. nov. exhibit caved-in portions or missing regions of shell below the apex (Figure 17). We interpret this to reflect the action of predators, indicating that this part of the animal was probably exposed above the sediment surface and thus exposed to predators (Figure 1).

### *Mellopegma* as Ancestor of Rostroconchs

Rostroconchs, bivalves, and Cambrian stenothechids such as *Mellopegma* share a ventrally curved lateral margin (Waller 1998) and significant lateral compression. In addition, Runnegar and Jell (1976) described rostroconch-like features in two internal molds referred to "*Mellopegma*?", that are not as laterally compressed as *M. georginense* or *M. schizocheras* sp. nov., but are otherwise similar in form. Both specimens have a shallow depression on the supra-apical end near the margin (Runnegar and Jell 1976, figure 8c7, 8c9). Runnegar and Jell (1976) interpreted this as a muscle insertion similar to what is seen in ribeirioid rostroconchs, a hypothesis that Waller (1998) said needs more testing. This feature is also seen in specimens of *Mellopegma simesi* (Figures 10.9-10; 11.3 with arrow) and *Stenothecha drepanoidea* (Figure 15.1, 15.8-9, 15.16-17 with arrows). Specimens of

**TABLE 3.** Data matrix for cladistic analysis. Characters and character states shown in Table 4.

|                                  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |   |
|----------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|---|
| <i>Oelandiella korobkovi</i>     | 0 | - | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  |   |
| <i>Watsonella</i> sp.            | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0  | 1  | 1  | ?  | 0  | 1  | 1  | 0  | 1  | 0  | 0  | 1  |   |
| <i>Anabarella plana</i>          | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0  | 1  | 1  | ?  | 0  | 1  | 1  | 0  | 1  | 0  | 0  | 1  |   |
| <i>Pojetaia runnegari</i>        | 0 | - | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0  | 1  | 1  | ?  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 1  |   |
| <i>Fordilla troyensis</i>        | 0 | - | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0  | 1  | 1  | ?  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 1  |   |
| <i>Mellopegma uslonicum</i>      | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  |   |
| <i>Mellopegma georginense</i>    | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  |   |
| <i>Acanthotheca junior</i>       | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0  | ?  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 1  |   |
| <i>Mellopegma simesi</i>         | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0  | ?  | 1  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  |   |
| <i>Tuarangia gravgaerdensis</i>  | ? | ? | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0  | ?  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |   |
| <i>Pseudomyona queenslandica</i> | ? | ? | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0  | ?  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  |   |
| <i>Ribeiria huckitta</i>         | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | 1  | 0  | 0 |

*Mellopegma* also show an incurved portion of the internal mold beneath the apex (best developed in *Mellopegma simesi*; Figure 11.11, 11.14) which Runnegar and Jell (1976) interpreted as a small pegma, the internal shell projection characteristic of rostroconchs.

Such observations led to speculation and debate about the role of *Mellopegma* in the early evolution of rostroconchs. Similarities between *Mellopegma* and early rostroconchs led Runnegar and Jell (1976) to postulate that *Mellopegma* is transitional between narrow early Cambrian forms such as *Anabarella* and rostroconchs, an idea echoed in Runnegar (1978), who referred to *Mellopegma* as a “pararostroconch.” In Wagner’s (1997) cladistic analysis (Figure 3), *Mellopegma/Eurekapegma* is transitional between other stenotheccids and a clade that includes bivalves and rostroconchs. In our cladistic analysis herein (Figure 4; Tables 3-4; Appendix 1), *Mellopegma* and *Acanthotheca* form a clade that is the sister group to a clade that comprises rostroconchs and *Pseudomyona/Tuarangia*.

Gubanov et al. (1999) described an alternative evolutionary sequence for the origin of rostroconchs, from *Oelandiella* through *Anabarella* to *Watsonella* in the early Cambrian of Siberia. Gubanov et al. (1999) argued that *Mellopegma* could not be considered ancestral to *Watsonella* because at the time *Mellopegma* was only known from the middle Cambrian whereas *Watsonella* is from the Tommotian. *Mellopegma* is now known from the early Cambrian (see above), but the assumption that *Watsonella* is the oldest rostroconch is now questioned.

More recent evidence suggests that *Watsonella* may be a quasi-bivalved helcionellid mollusc, not a rostroconch. The closer relationship of *Watsonella* to bivalves than rostroconchs is supported by Dzik’s (1994, figure 12g) observation of a divided larval shell in *Watsonella*, similar to bivalves but dissimilar to rostroconchs. The idea that *Watsonella* is not a rostroconch but that it may be ancestral to bivalves has received recent support (Runnegar 1996; Wagner 1997; Carter 2001), although other specimens of *Watsonella* appear to have an undivided or incompletely divided larval shell (AVK, personal observation). More work is needed to better elucidate the range of form in this important genus.

The middle Cambrian *Acanthotheca junior* has also been interpreted as a rostroconch (Runnegar 1996), but this species lacks the breakdown of coiling and anterior-posterior elongation of shell that characterize ribeirioid rostroconchs, and the greatest width of *Acanthotheca* occurs in the supra-apical region of the shell, not the sub-apical region as in rostroconchs. If neither *Watsonella* nor *Acanthotheca* are rostroconchs, then the oldest known members of this class are from the early late Cambrian.

Runnegar (1996) proposed a morphological transition between laterally compressed stenotheccids like *Stenothecca* and *Mellopegma* through *Acanthotheca junior* to younger ribeirioid rostroconchs. The occurrence of calcitic semi-nacre in *Acanthotheca junior* (Runnegar, 1996) from the Gowers Formation (Vendrasco et al. 2010, pl. 3, figs. 1, 6-9, 24) is an additional similarity to *Mellopegma*, adding to others such as a curved ventral margin, a pegma, and a slight coil. These similarities suggest



**TABLE 4.** Summary of characters and character states for cladistic analysis.

| Character                               | States                    |                                |        |
|---|---------------------------|--------------------------------|--------|
|   | 0                         | 1                              | 2      |
| 1 Pegma or pegma-like structure         | Absent                    | Present                        |        |
| 2 Development of pegma                  | Weak                      | Moderate                       | Strong |
| 3 Divided shell                         | Absent                    | Present                        |        |
| 4 Degree of coiling                     | Up to 1 coil              | 1 or more coils                |        |
| 5 Raised sub-apical aperture lip        | Absent                    | Raised lip or siphon           |        |
| 6 Internal shell ridges                 | Absent or faint           | Present                        |        |
| 7 Curved ventral margin                 | Absent                    | Present                        |        |
| 8 Univalved or bivalved larval shell    | Univalved                 | Bivalved                       |        |
| 9 Lateral compression                   | Absent                    | Present                        |        |
| 10 Ratio of length:height               | Less than 1.5             | 1.5 or more                    |        |
| 11 Prismatic shell layer                | Absent                    | Present                        |        |
| 12 Inner laminar layer                  | Absent                    | Present                        |        |
| 13 Inner calcite layer                  | Absent                    | Present                        |        |
| 14 Shell pores                          | Absent                    | Present                        |        |
| 15 Spiny layer (lamello-fibrillar)      | Absent                    | Present                        |        |
| 16 Stepwise inner layer                 | Absent                    | Present                        |        |
| 17 Calcitic semi-nacre                  | Absent                    | Present                        |        |
| 18 Prismatic best preserved near apex   | Absent                    | Present                        |        |
| 19 Coiling loss; straight dorsal margin | Absent                    | Present                        |        |
| 20 Aperture constriction                | Absent                    | Pinched near sub-apical margin |        |
| 21 Aperture shape                       | Sub-apical width greatest | Supra-apical width greatest    |        |

a close relationship between *A. junior* and *Mellopegma*. In particular, a transitional sequence can be envisioned from a form like *Mellopegma schizocheras* sp. nov. through a form like *Mellopegma simesi* to *Acanthotheca junior*. *M. simesi* is intermediate with respect to elongation, lateral compression, flaring of sub-apical margin, and development of the pegma. In addition, these three taxa share a similar pattern of shell microstructure (Vendrasco et al. 2010).

Although *Mellopegma* and *Acanthotheca* lack the uncoiled nature of the shell that characterizes rostroconchs, the stenothecid *Eurekapegma*, the youngest member of the lineage, has a range in form from slightly coiled as is typical for *Mellopegma* to uncoiled, typical for ribeirioid rostroconchs (MacKinnon 1985, figure 3k, o, q, u, w). Thus *Eurekapegma* has a form that may represent the ancestral state to rostroconchs.

The shell microstructure of ribeirioid rostroconchs is unknown if *Acanthotheca junior* is considered outside the group. Such information would help in testing the hypothesis that stenothecids are ancestral to rostroconchs. Shell microstructure is known from the Carboniferous conocardioid *Apotocardium*, shown to have a fine prismatic

outer layer, crossed lamellar middle layer, and porcellaneous/matted inner layer (Rogalla et al. 2003). This configuration differs significantly from that of *Mellopegma* and its kin, although there are some parallels with what occurs in *Anabarella* and *Watsonella* (Kouchinsky 1999; Rogalla et al. 2003). Peel (2004) noted the striking difference between the protoconchs of ribeirioids and conocardioids, indicating that these two rostroconch groups may have had independent origins from different types of helcionellids. In Peel's (2004) model a group of exogastric helcionellids gave rise to ribeirioids whereas endogastric forms gave rise to conocardioids. The possible polyphyly of the Rostroconchia may help explain the difference in shell microstructure between conocardioids and the stenothecids that may have been ancestral to ribeirioids.

MacKinnon (1985) argued that the middle Cambrian *Enigmaconus* may have been ancestral to rostroconchs. *Enigmaconus* has distinct pegma-like structures similar to what occurs in rostroconchs, structures that MacKinnon suggested originated in rostroconchs prior to lateral compression. However, there appears to be convergent evolution in the development of pegma-like structures (Runnegar 1996), as well as other rostroconch charac-

ters such as elongation/scaphopodization (Peel 2006) and a breakdown in coiling (in *Eotebenna*, *Pseudomyona*, *Eurekapegma*, and rostroconchs). Conflicting evidence typifies all the possible ancestors of rostroconchs, including:

*Watsonella*: the split shell, pegma-like structure underneath the apex, and overall shape—including curved ventral margin—are consistent with rostroconchs, but the significant stratigraphic gap between it and undoubted rostroconchs is evidence against this link. The apparent split larval shell likewise is evidence against the link between *Watsonella* and rostroconchs, although Dzik's (1994) interpretation of the juvenile shell in *Watsonella* has been questioned by Rogalla et al. (2003), and other specimens of *Watsonella* appear to have a univalved juvenile shell (AVK, personal observations).

*Enigmaconus*: pegma-like structures are present and in the same general areas as in rostroconchs, but this form is much wider than rostroconchs and lacks the curved ventral margin. Moreover, the unusual scaly shell microstructure in *Enigmaconus* (Kouchinsky 2000a) is quite different from the known microstructure of *Apotocardium*.

*Pseudomyona*/*Tuarangia*: pseudobivalved, laterally compressed, uncoiled shell like rostroconchs, but without pegma. Although these taxa differ from typical ribeirioids in being taller and having a more centrally located larval shell, they share with ribeirioids other aspects of form: for example, loss of coiling/straight dorsal margin and lack of aperture constriction—characters not seen in stenothecids (Figure 4; Tables 3-4; Appendix 1). The inner shell microstructure of foliated calcite has the same mineralogy as stenothecids, but this is different from the known microstructure of *Apotocardium*. Wagner (1997) argued that *Pseudomyona* and *Tuarangia* are more closely related to rostroconchs than is *Watsonella*, noting that *Pseudomyona*, *Tuarangia*, and undisputed rostroconchs share denticles and an extensive elongation of the anterior part of the shell.

*Acanthotheca* gen. nov./*Mellopegma*/*Eurekapegma*: these taxa share the same curved ventral margin and lateral compression as rostroconchs. However, they lack a pegma and have a shell microstructure different from *Apotocardium*. Moreover, they show coiling unlike rostroconchs, although some specimens of *Eurekapegma* lost coiling and are very similar in overall appearance to ribeirioid rostroconchs.

The origin of rostroconchs remains a mystery. Shell microstructure data from some of the earliest

undisputed rostroconchs would provide evidence for or against the hypotheses described above, but so far this information is lacking.

### Origin of Bivalves

The morphology and stratigraphy of the earliest bivalves, stenothecids, undisputed rostroconchs, and *Watsonella* are consistent with the hypotheses that *Watsonella* or a close relative gave rise to bivalves and a different helcionellid gave rise to rostroconchs. In addition to significant lateral compression and a curved ventral margin, stenothecids and *Watsonella* share with bivalves a number of similarities, including an extended sub-apical dorsal ridge (anterior in bivalves), and an inner shell microstructure that is laminar, sheet-like, and composed of highly organized sub-units (see "Shell microstructure" above).

*Pojetaia* and *Fordilla*, taxa that appear to be the earliest bivalves (Pojeta 2000), may have originated from a genus like *Watsonella*, a taxon that is either a stenothecid (Parkhaev in Gravestock et al. 2001) or descended from one (*Anabarella*; Kouchinsky 1999). Dzik's (1994) observation of a split shell in *Watsonella* has shifted the predominant view of this genus from being a rostroconch to an ancestor of bivalves.

Additional support for a link between *Watsonella* and bivalves comes from Carter (2001), who noted similarities between the shell microstructure of *Watsonella* and *Anabarella* (described by Kouchinsky 1999) and that of the earliest bivalves *Fordilla* and *Pojetaia*. The putative earliest bivalves had an equivocal microstructure interpreted as prismatic (Runnegar 1985) or large tablet nacre (Carter 2001). Carter (2001) noted a similar microstructure in *Anabarella* and *Watsonella* that he likewise classified as large tablet nacre, strengthening the argument that these taxa are ancestral to bivalves. This shell microstructure is different than the calcitic semi-nacre of *Mellopegma*.

The Cambrian taxa *Pseudomyona* and *Tuarangia* have been considered questionable bivalves (Pojeta 2000, Carter 2001, Elicki and Gürsu 2009) in spite of superficial similarities in form such as a bivalved or pseudo-bivalved shell. They have a foliated calcite inner shell microstructure (Runnegar 1985), which is more similar to the calcitic semi-nacre of *Mellopegma* than to the laminar inner shell microstructure of *Watsonella*, *Fordilla*, or *Pojetaia*. Hinz-Schallreuter (1995, 2000) considered *Tuarangia* a bivalve and *Pseudomyona* a rostroconch, but the striking similarities between *Tuarangia* and *Pseudomyona* indicate they are closely related

(Runnegar and Pojeta 1992). The nature of the relationships of *Pseudomyona* and *Tuarangia* to bivalves and rostroconchs is unresolved.

Runnegar (1996) suggested *Watsonella* may have been a link between stenotheacid monoplacophorans and the Bivalvia. He also argued that the long dorsal margin of laterally compressed univalves such as *M. georginense* was the precursor to the bivalve ligament. Likewise, Wagner (1997) suggested *Watsonella* (as *Heraultipegma*) is not a rostroconch but instead is on the lineage leading to bivalves.

The stratigraphy of these fossils is consistent with the hypotheses that *Watsonella* or a close relative gave rise to bivalves and a different helcionellid, possibly *Mellopegma*, gave rise to rostroconchs. *Watsonella* occurs in the *N. sunnaginicus* Biozone of the Tommotian Stage and in beds likely deposited earlier in Siberia, China, and Avalonia (lower Stage 2). In fact, *Watsonella* was suggested as an index fossil for the base of Stage 2. *Mellopegma indecorum* co-occurs with *Watsonella* in samples M303/2 (basal Petrotsvet Formation; Rozanov et al. 1969) and 183e (Rassokha River; Egorova and Savitzky 1969). The earliest bivalves *Fordilla* and *Pojetaia* are known from the lower Stage 3 (Elicki and Gürsu 2009). In contrast, the oldest rostroconchs are from the early late Cambrian.

## CONCLUSIONS

Based on our analyses of *Mellopegma* and other stenotheacids, we conclude that: (1) calcitic semi-nacre probably occurred in the early Cambrian *Mellopegma uslonicum*, extending back the first appearance of this unusual type of shell microstructure and thereby providing additional support for a fundamental homology between the shell of brachiopods and early molluscs; (2) the periostracum was present in middle Cambrian *Mellopegma* and other molluscs; (3) the protoconchs of *Mellopegma* reveal that these shells were likely adults and that this genus was lecithotrophic; and (4) stenotheacids like *Mellopegma* appear to have been increasingly under predation pressure from the early to middle Cambrian and in response became better adapted to avoid predation, suggesting an early arms race between predators and their molluscan prey.

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## APPENDIX 1.

Detailed description of characters and character states for cladistic analysis herein.

### 1. Pegma or pegma-like structure.

**Description:** projection angled inward from near the apex.

**States:** (0) Absent; (1) Present.

**Notes:** *Pseudomyona* and *Tuarangia* appear to have tooth-like structures projecting from the dorsal margin of their shell plates (Runnegar and Pojeta 1992, fig. 3c). It is unclear to what extent these structures might be homologous to the pegma, and thus these two genera are coded for this character with “?” (unknown state).

### 2. Development of pegma.

**Description:** extent of inward projection of pegma or pegma-like structure.

**States:** (-) Not applicable (for those without pegma); (0) Weak (wide but short extension inward); (1) Moderate (greater extension inward, reflected on internal moulds as a groove); (2) Strong (extensive development inward as a sheet).

### 3. Divided shell.

**Description:** univalved or bivalved adult shell, regardless of state of larval shell.

**States:** (0) Absent (univalved shell); (1) Present (bivalved shell).

### 4. Degree of coiling.

**Description:** extent of coiling, whether just in apical region or throughout the shell.

**States:** (0) Up to one complete coil; (1) One or more coils.

### 5. Raised sub-apical aperture lip.

**Description:** raised edge of aperture underneath the apex, allowing part of the aperture to face horizontally.

**States:** (0) Absent; (1) Present.

### 6. Internal shell ridges.

**Description:** comarginal ridges on the inner surface of the shell, reflected in internal moulds.

**States:** (0) Absent or very faint; (1) Present.

### 7. Curved ventral margin.

**Description:** ventral (aperture) margin raised at anterior and posterior ends.

**States:** (0) Absent (no significant curvature); (1) Present.

### 8. Univalved or bivalved larval shell.

**Description:** whether larval shell is split into two or is univalved, regardless of state of adult shell.

**States:** (0) univalved; (1) bivalved larval shell.

**Notes:** *Watsonella* is coded as having a bivalved larval shell, even though there is some doubt as to how widespread such a state is for this genus (see main text).

### 9. Lateral compression.

**Description:** shell with much greater height than width.

**States:** (0) Absent; (1) Present.

### 10. Ratio of length: height.

**Description:** whether l:h of shell is less or greater than 1.5.

**States:** (0) Less than 1.5; (1) 1.5 or greater.

### 11. Prismatic shell layer.

**Description:** prismatic microstructure in one of the shell layers. Prismatic shell microstructure consists of “mutually parallel, adjacent polygonal columns that do not strongly interdigitate along their mutual boundaries, and which may be separated by organic matrix” (Carter et al. 1990, p. 654).

**States:** (0) Absent; (1) Present.

**Notes:** taxa coded as 1 in this analysis have distinct imprints of prismatic shell microstructure somewhere on the internal moulds. Others are coded as “?” (uncertain) because prismatic shell microstructure is typically in the outer shell layer of molluscs, and consequently many species that have it will not typically show it on internal moulds.

### 12. Inner laminar layer.

**Description:** inner shell layer (reflected on most regions of surface of internal mould) is a laminar (layered) form wherein “rods, laths, blades or tablets comprise sheets which are oriented parallel or nearly parallel to the depositional surface” (Carter et al. 1990, p. 611).

**States:** (0) Absent; (1) Present.

### 13. Inner calcite layer.

**Description:** inner shell layer with calcitic mineralogy.

**States:** (0) Absent; (1) Present.

#### 14. Shell pores.

**Description:** shell pores, reflected on internal moulds as tubercles.

**States:** (0) Absent; (1) Present.

#### 15. Lamello-fibrillar (spiny)

**Description:** presence within shell of layers that consisted of organized fibres where “the horizontal fibers in successive laminae differ in orientation by irregularly varying angles” (Carter et al. 1990, p. 611). This is the “spiny” shell microstructure of Kouchinsky (1999).

**States:** (0) Absent; (1) Present.

#### 16. Stepwise inner layer.

**Description:** inner shell layer with unusual laminar shell microstructure named ‘stepwise’ by Kouchinsky (1999).

**States:** (0) Absent; (1) Present.

#### 17. Calcitic semi-nacre.

**Description:** presence in the shell of laminae made up of calcite rhombs that laterally grew together.

**States:** (0) Absent; (1) Present.

#### 18. Prismatic best preserved near apex.

**Description:** expression of the most distinct prismatic shell microstructure on the inner surface of the shell (hence reflected on internal moulds) near the apex rather than elsewhere on the surface.

**States:** (0) Absent; (1) Present.

#### 19. Coiling loss; straight dorsal margin.

**Description:** whether coiling of the adult shell continues from the initial coiling of the larval shell or whether the coiling is lost, forming a straight dorsal margin instead.

**States:** (0) Absent (coiled); (1) Present (forming straight margin).

#### 20. Aperture constriction.

**Description:** lateral constriction (pinching) of shell aperture near sub-apical margin, with a widening of the aperture front and back of it.

**States:** (0) Absent (1) Present (pinched).

#### 21. Aperture shape.

**Description:** whether the greatest width of aperture occurs more towards the anterior or posterior end. However, because anterior and posterior are still somewhat speculative with these fossils, this character is defined with respect to the apex.

**States:** (0) Sub-apical width greatest; (1) Supra-apical width greatest.

## APPENDIX 2.

Early Cambrian (up to Botoman Stage) molluscs with evidence for shell pores, including the

sources of information. This list was modified from that in Parkhaev (2006).

| <b>Taxon</b>                     | <b>Nature of evidence</b>       | <b>Source(s)</b>  |
|----------------------------------|---------------------------------|---|
| <i>Mellopegma uslonicum</i>      | Large, tapered tubercles        | Kouchinsky 2000a; Parkhaev 2006                           |
| <i>Yochelcionella</i> sp.        | Shallow tubercles               | Kouchinsky 2000a  |
| <i>Mackinnonia anabarica</i>     | Large tubercles                 | Kouchinsky 2000a; Parkhaev 2006                           |
| <i>Auricullina papulosa</i>      | Large tubercles                 | Kouchinsky 2000a; Parkhaev 2006                           |
| <i>Auricullina granulosa</i>     | Elongate, cylindrical tubercles | Parkhaev 2006   |
| <i>Postacanthella elegans</i>    | Conical tubercles               | Xing et al. 1984; Parkhaev 2006                           |
| <i>Postacanthella</i> sp.        | Large tubercles                 | Kouchinsky 2000a; Parkhaev 2006                           |
| <i>Tuberoconus paucipalillae</i> | Large tubercles                 | Xing et al. 1984; Parkhaev 2006                           |
| <i>Daedalia daedala</i>          | Conical tubercles               | Gravestock et al. 2001; Parkhaev 2006                     |
| <i>Anhuiconus microtuberus</i>   | Small tubercles                 | Zhou and Xiao 1984; Gravestock et al. 2001; Parkhaev 2006 |
| <i>Leptostega hyperborea</i>     | Small tubercles                 | Parkhaev 2006   |
| <i>Philoxenella spiralis</i>     | Tubercles plus columns          | Parkhaev 2006   |
| <i>Khairkania rotata</i>         | Columns                         | Parkhaev 2006   |
| <i>Barskovia hemisymmetrica</i>  | Tubercles plus columns          | Parkhaev 2006; personal observation                       |
| <i>Nomgoliella australiensis</i> | Tubercles plus columns          | Gravestock et al. 2001; Parkhaev 2006                     |