

# Chapter 2

## Ultra-elongate Freshwater Pearly Mussels (Unionida): Roles for Function and Constraint in Multiple Morphologic Convergences with Marine Taxa

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### Contents

2.1	Introduction.....	22
2.2	Morphologic Features of Ultra-elongate Taxa .....	27
2.2.1	Marine Exemplars .....	27
2.2.2	Ultra-elongate Unionida.....	29
2.3	Modes of Differential Shell Growth in Ultra-elongate Bivalves .....	31
2.4	Substrate Preferences and Characteristics of Domicinia in Ultra-elongate Bivalves .....	34
2.4.1	Marine Taxa .....	34
2.4.2	Field Observations of Mycetopodidae in the Upper Amazon Basin (Peru).....	36
2.4.3	Other Ultra-elongate Unionoids.....	38
2.5	Discussion.....	39
2.6	Conclusions.....	41
	References.....	42

**Abstract** Morphologic convergence may arise because natural selection produces an optimal solution for a given set of environmental conditions or because constructional and historical constraints limit available variation, making certain morphologies inevitable. Shell shape in bivalves typically is interpreted as functional, with emphasis placed on substrate preferences and life habits. Freshwater pearly mussels (Order Unionida) represent the most diverse freshwater bivalve clade and, although their life history and related morphologic traits are strikingly divergent from marine bivalves as well as other freshwater bivalve clades, multiple convergences in shell form within and among these groups occur. Ultra-elongate shells (length/height ratios  $>3.0$ ) in both marine and unionoid taxa are one such example. At least 13 families, including 4 phylogenetically defined unionoid families, have ultra-elongate representatives. These taxa occur in substrates ranging from soft sediments to hard grounds and a variety of life habits including nonmotile semi-infaunal, active burrowers, and borers; which seems to imply weak functional/adaptive control on

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morphology. For many of these taxa, however, this shape may reflect functional forces related to direct substrate penetration without major anterior/posterior rotation of the shell, rather than the type of substrate penetrated. Further, shell elongation is achieved through a variety of differential growth patterns, which argues against a strong role for constructional or historical constraint. Clarifying the meaning of a modern analog or proxy is critical for evaluating paleoenvironmental and paleoecological interpretations of extinct ultra-elongate bivalve taxa as well as for informing efforts to protect and restore extinction-vulnerable extant populations.

**Keywords** Unionida · Convergence · Morphology · Constraint · Function · Substrate · Life-habit · Differential growth

## 2.1 Introduction

Function is commonly assigned to morphologic features because it is through phenotype that organisms interact with their environment. Nonetheless, evolutionary history leaves a record in the morphology of clades and, without this legacy, we could not use morphologic data alone to distinguish between homology and homoplasy, the latter arising either from parallelism (nonhomologous similarities that are the product of the same developmental genetic mechanisms) or convergence (nonhomologous similarities that are the product of different developmental genetic mechanisms) (see Wake et al. 2011). Therefore, we harness the mosaic nature of evolution to both reconstruct evolutionary relationships and understand function and adaptation. In other words, we view phenotype as resulting from the interplay of functional, constructional, and historical factors (e.g., Seilacher 1984; Savazzi 1987; Gould 2002; Cubo 2004; Schwenk and Wagner 2004; Brakefield 2006; Losos 2011).

The roles of function and history are apparent in the freshwater pearly mussels (Order Unionida). This clade represents an ancient invasion and major radiation into freshwater with members occurring on all continents except Antarctica. The Unionida includes 840 valid extant nominal species (Graf and Cummings 2007; Bogan and Roe 2008) and has a fossil record that extends to the Triassic (Watters 2001; Bogan and Roe 2008). Graf and Cummings (2006) recognized eight morphologic and/or life-history synapomorphies for the order, most of which relate to adaptations for reproduction in flowing waters, including both brooding and parasitic larval stages. The evolutionary history of unionoids, on the other hand, is readily apparent based on features such as the distinctive schizodont dentition of both this order (unless lost secondarily) and its sister taxon, the marine Trigoniida (Graf and Cummings 2006 and references therein).

Although many life history and morphologic traits in unionoids are unique to the clade, striking examples of convergence (used here to refer both to parallelism and convergence *sensu stricto*; see Wake et al. 2011) in shell form occur between unionoids and other bivalves. One such example is that of the freshwater “oysters” in the Etheriidae that cement their valves to hard substrates and whose shells

converge on the morphology of marine oysters (Yonge 1962; Graf and Cummings 2006). A cementing freshwater veneroid, *Posostrea anomioides* (Cyrenidae = Corbiculidae, see Bieler et al. 2010) also has been described (Bogan and Bouchet 1998).

Extremely elongate unionoid species (here defined as having length/height ratios  $> 3.0$  and referred to as ultra-elongate taxa) are another putative example of marine/freshwater convergence (Savazzi and Yao 1992; Haag 2012). In fact, several ultra-elongate unionoids have been compared, at least implicitly, to marine razor clams (Solenidae and Pharidae) through the use of scientific names that include *Solenia*, *Lamproscapha ensiformis*, and *Mycetopoda soleniformis*. Some of these taxa (*Mycetopoda* spp., *Solenia*) not only possess shells similar in shape to razor clams, but also exhibit an anteriorly directed, distally enlarged foot reminiscent of *Solen* and *Ensis*.

Ultra-elongate taxa, however, are not limited to a few clades or to a narrow range of habitats in either marine or freshwater environments. In the marine realm, ultra-elongate shells characterize razor clams, but also occur in extant genera of the Solecurtidae (*Tagelus*), Mytilidae (*Lithophaga*, *Adula*, *Mytella*, *Arcuatula*, *Adipicola*, and *Gigantidas*), Pholadidae (*Pholas*), Nuculanidae (*Poroleda*, *Propeleda*, and *Adrana*), Petricolidae (*Petricolaria*), Vesicomysidae (*Elenaconcha extenta*), and Arcidae (*Litharca*). Further, ultra-elongate morphologies occur in substrates ranging from soft sediment to hard grounds (rock, shell, and wood), and include active burrowers, borers, and byssally attached species.

Ultra-elongate unionoids also are represented in multiple clades, occurring in ten genera from eight subfamilies and four families (Table 2.1; Fig. 2.1) that include the Unionidae (*Arconaia*, *Cuneopsis*, *Lanceolaria*, *Solenia*, *Elliptio*), Hyriidae (*Lortella*), Iridinidae (*Chelidonopsis*), and Mycetopodidae (*Mycetopoda*, *Mycetopodella*, *Lamproscapha*). The ultra-elongate shape arose at least seven times within the order, based on phylogenetic placement of genera containing ultra-elongate species (Fig. 2.1; Table 2.1; also see Graf 2013).

This chapter explores functional interpretations of shell shape by summarizing available information on environmental occurrences, life habits (e.g., epifaunal/semi-infaunal, burrowing, burrow dwelling, borehole dwelling), and burrowing/boring behavior of both marine and freshwater ultra-elongate taxa, including a detailed description of the occurrence of ultra-elongate unionoids collected from three tributaries of the upper Amazon River in southeastern Peru. The various modes of differential growth that produce ultra-elongate shells are outlined, as indicated through differences in beak position, muscle scar shape, and hinge development.

A better understanding of the ecology of these unionoid bivalves can inform efforts to protect and restore their extant populations, as pearly mussels are the most critically endangered bivalve clade on a global scale (e.g., Bogan 1993; Lydeard et al. 2004). In fact, for the 499 unionoid species listed on the International Union for Conservation of Nature (IUCN) Red List 2012.2 (<http://www.iucnredlist.org/>), 41% are considered threatened (175) or extinct (29), and data are insufficient to evaluate the status of an additional 94 species (18.9%), with some ultra-elongate species threatened by habitat destruction and/or introduction of invasive species (Mansur et al. 2003; Castillo et al. 2007). In addition, a general understanding of the

**Table 2.1** Unionoid genera with extant ultra-elongate species

Family (subfamily)	Genus	L/H	Environmental occurrence	Geographic distribution genus	Ultra-elongate species included in published molecular phylogeny
Unionidae (Unioninae)	<i>Arconaia</i>	4.9	<i>A. lanceolata</i> : organic-rich, anoxic lake muds (Savazzi and Yao 1992)	Asia	<i>A. lanceolata</i> : Huang et al. 2002; Zhou et al. 2007
Unionidae (Unioninae)	<i>Cuneopsis</i>	3.1	<i>C. celtiformis</i> and <i>C. pisciculus</i> : active burrowers in well oxygenated lake and river channel sediment (Savazzi and Yao 1992)	Asia	<i>C. celtiformis</i> : Zhou et al. 2007 <i>C. pisciculus</i> : Huang et al. 2002; Zhou et al. 2007
Unionidae (Unioninae)	<i>Lanceolaria</i>	4.2	<i>L. grayana</i> : active burrower in well oxygenated lake and river channel sediment (Savazzi and Yao 1992); mudbanks at mouth of streams flowing into Luc Nam River at low water (Dautzenberg and Fischer 1905)	Asia	<i>L. grayana</i> : Huang et al. 2002; Ouyang et al. 2011; <i>L. gladiola</i> : Ouyang et al. 2011
Unionidae (Ambleminae)	<i>Elliptio</i>	4.1 <sup>1</sup>	<i>E. shepardiana</i> : along stable protected river and stream banks with fine sand and silt, behind roots and around logs and trees (University of Georgia Museum of Natural History 1996)	North America	<i>E. shepardiana</i> : Campbell and Lydeard 2012
Unionidae (Indotropical "Gonideinae")	<i>Solenaia</i>	4.2	<i>S. iridinea</i> (as <i>S. oleivora</i> ): in anoxic lake muds with high methane content (Savazzi and Yao 1992) <i>S. soleniformis</i> (as <i>Balwantia soleniformis</i> ): bores into firm grounds in river cutbanks (Godwin-Austen 1919)	Asia	<i>S. iridinea</i> : Huang et al. 2002; Ouyang et al. 2011 (as <i>S. carinatus</i> , <i>S. oleivora</i> , and <i>S. rivularis</i> )
Hyriidae (Velsioninae)	<i>Lortietta</i>	3	<i>L. rugata</i> : under rocks and ledges, among roots and mud; in tube-like burrows in mudbanks (Ponder and Bayer 2004)	Australia	<i>L. rugata</i> : Graf and Cummings 2006

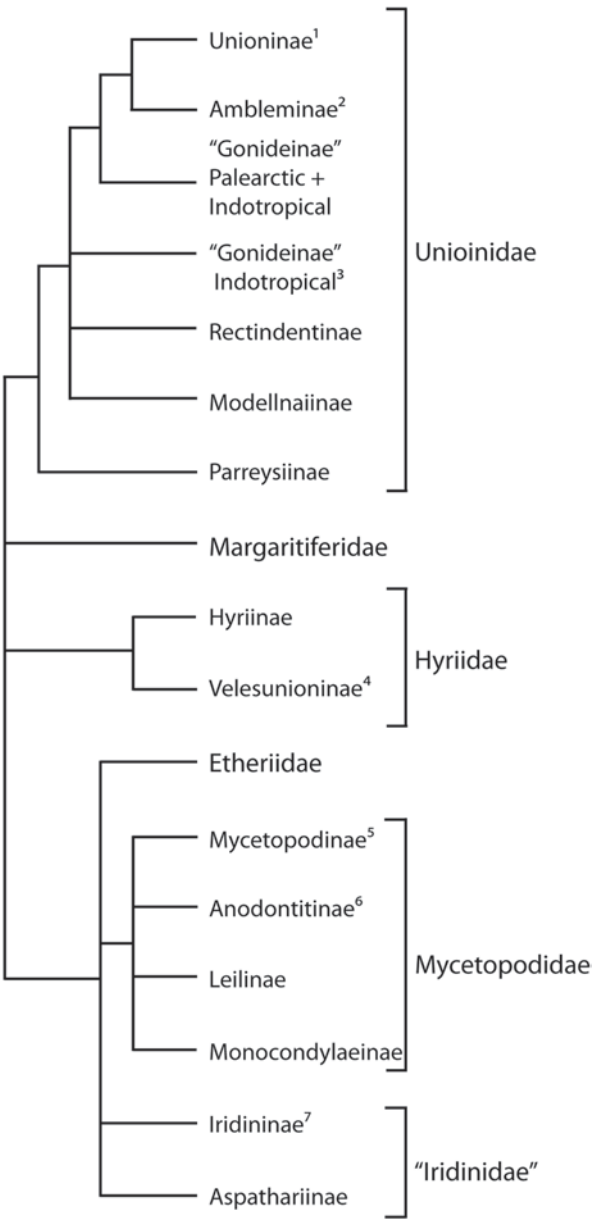
**Table 2.1** (continued)

Family (subfamily)	Genus	L/H	Environmental occurrence	Geographic distribution genus	Ultra-elongate species included in published molecular phylogeny
Mycetopodidae (Mycetopodinae)	<i>Mycetopoda</i>	3.3	<i>Mycetopoda</i> : in permanent domichnia in firm grounds exposed in river banks and rapids (d'Orbigny 1846; Veitenheimer and Mansur 1978). <i>M. siliquosa</i> : in mud (Castillo et al. 2007) lake margins and stream channels in soft sediment (Pimpão et al. 2008; pers. obs.) <i>M. legumen</i> : in fine compacted sand in rivers (Veitenheimer and Mansur 1978) <i>Mycetopoda soleniformis</i> : in firm grounds exposed in river banks and rapids (Burmeister 1988; pers. obs.)	South America	<i>S. siliquosa</i> : Whelan et al. 2011
Mycetopodidae (Mycetopodinae)	<i>Mycetopodella</i>	4.3	<i>Mycetopodella falcata</i> : in permanent domichnia in firm grounds exposed in river banks and rapids (Burmeister 1988; pers. obs.)	South America	No
Mycetopodidae (Anodontitinae)	<i>Lamproscapha</i>	3.8	<i>L. ensiformis</i> : channels within large channel-bar complex at convergence of Rios Negro, Amazonas and Solimões (Pimpão et al. 2008)	South America	No
"Iridinidae" (Iridininae)	<i>Chelidonopsis</i>	4	<i>C. hirundo</i> : sandy and gravelly river bottoms just below or above rocky barriers, Congo Basin (Pilsbry and Bequaert 1927)	Africa	No

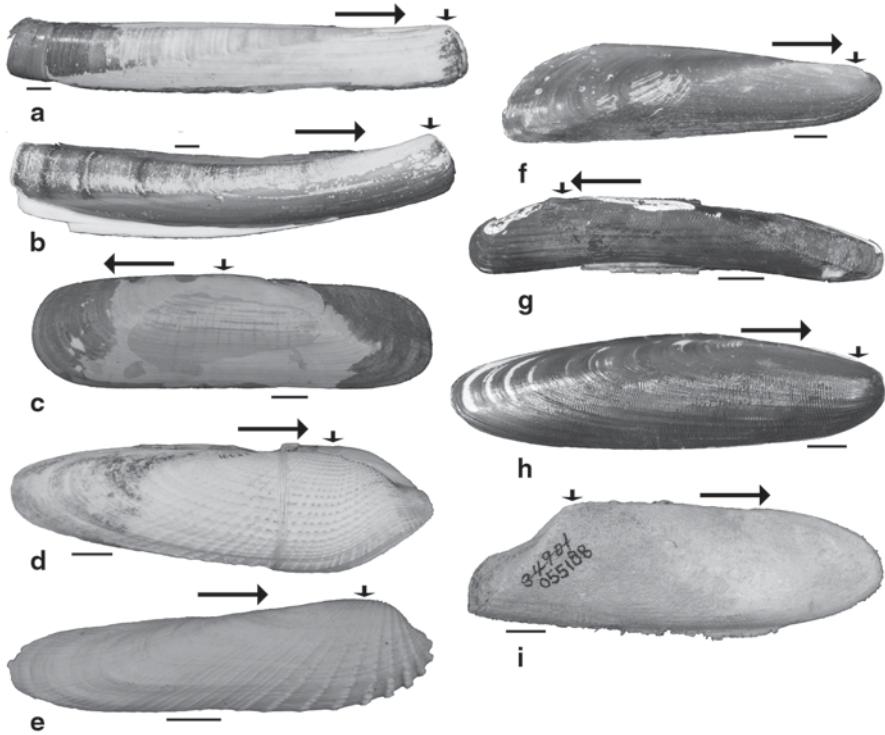
Length/height (L/H) values are taken from figures illustrated by Haas (1969) unless otherwise indicated by a superscript. Phylogenetic placement based on Graf (2013). Higher taxa in quotations are not monophyletic as they are currently defined (see Graf and Cummings 2006; Whelan et al. 2011). Species identifications follow that of Graf and Cummings (2007) and the Mussel Project Website (<http://mussel-project.uwsp.edu/index.html>)

<sup>1</sup> From Haag (2012)

**Fig. 2.1** Phylogenetic relationships among families and subfamilies of the Order Unionida, based on Graf (2013). Taxon names in quotations are paraphyletic as they are currently defined. *Superscript numbers* indicate the presence of genera with ultra-elongate species within the subfamily as follows: <sup>1</sup>*Arconaia*, *Cuneopsis*, and *Lanceolaria*; <sup>2</sup>*Elliptio*; <sup>3</sup>*Sole-naia*; <sup>4</sup>*Lortiella*; <sup>5</sup>*Mycetopoda* and *Mycetopodella*; <sup>6</sup>*Lampro-scapha*; and <sup>7</sup>*Chelidonopsis*. This distribution of ultra-elongate taxa indicates a conservative estimate of seven independent acquisitions of this shell morphology



role of function and constraint in producing ultra-elongate shapes is useful in evaluating confidence in paleoenvironmental and paleoecologic interpretations of extinct ultra-elongate taxa such as species of *Prothyris* (L:H 3.0 in *P. elegans*), *Cercomya* (L:H 3.4 in *C. pinguis*), *Palaeosolen* (L:H 5.2 in *P. siliquoidea*), or *Pseudarca* (L:H 4.1 in *P. typa*).



**Fig. 2.2** Examples of ultra-elongate marine taxa. Scale bars = 1 cm. *Horizontal arrows* point toward the anterior of each shell. *Vertical arrows* indicate the position of the beak. **a** *Solen vagina* (Ireland). **b** *Ensis directus* (Maine). **c** *Tagelus californianus* (California). **d** *Pholas dactylus* (Spain). **e** *Petricolaria pholadiformis* (The Netherlands). **f** *Mytella speciosa* (Peru). **g** *Adula falcata* (California). **h** *Lithophaga gracilis* (Japan). **i** *Litharca lithodomus* (Ecuador). All images are of specimens in the Invertebrate Zoology collections of the California Academy of Sciences

## 2.2 Morphologic Features of Ultra-elongate Taxa

### 2.2.1 Marine Exemplars

Among extant marine bivalves, most ultra-elongate species are either razor clams or boring bivalves (Table 2.2; Fig. 2.2), and shape similarities among these taxa have previously been considered convergent (Yonge 1955; Savazzi 1999). Most members of the Solenidae and Pharidae have L:H ranging from about 3 to over 7, with parallel-sided, straight to arched dorsal and ventral margins; indistinct umbos at the shell anterior; and near-vertical anterior and posterior margins (Fig. 2.2a, b). Species of *Tagelus* (Solecurtidae; commonly called stout razor or jack-knife clams) have similar morphologies to the Solenidae and Pharidae (elongate–quadrate), although generally they are not as elongate (L:H ~3), and have the beak located at the valve midline (Fig. 2.2c). In addition, all these bivalves are distinctive in possessing

**Table 2.2** Exemplar taxa for extant marine genera with ultra-elongate species

Family	Genus	L/H	Substrate occurrences and domichnia, if reported in literature
Nuculanidae	<i>Adrana</i> (11)	3.5 <sup>1</sup>	<i>A. patagonica</i> : in muddy sand (Saavedra et al. 1999)
	<i>Poroleda</i> (3)	3.3	<i>P. spathula</i> : in sand (Grove 2011) <i>P. lanceolata</i> : in mud (Powell 1979)
	<i>Propeleda</i> (8)	3.4	<i>P. platessa</i> : in sandy mud (Nijssen-Meyer 1972)
Mytilidae	<i>Adipicola</i> (9)	4.3 <sup>1</sup>	<i>A. iwaotakii</i> : epifaunal or infaunal byssate on wood, at whale falls and at hydrothermal vents (Owada 2007; Kyuno et al. 2009; Lorion et al. 2009)
	<i>Adula</i> (7)	5.4	<i>A. falcata</i> : bores into soft mudstone (Yonge 1955; Owada 2007)
	<i>Arcuatula</i> (11)	3.1 <sup>1</sup>	<i>Arcuatula</i> : byssally attached semi-infaunal in mud (Grove 2011)
	<i>Gigantidas</i> (3)	3.4 <sup>1</sup>	<i>G. sharikoshii</i> : semi-infaunal in sand (Hashimoto and Yamane 2005)
	<i>Lithophaga</i> (19)	3.1	<i>L. plumula</i> : bores into calcareous rocks (Yonge 1955)
	<i>Mytella</i> (4)	3.5 <sup>1</sup>	<i>M. speciosa</i> : byssally attached semi-infaunal among mangrove roots (Riós-Jara et al. 2009; Santos et al. 2010)
Acridae	<i>Litharca</i> (1)	3.5	<i>L. lithodomus</i> : bores into sandstone (Nicol and Jones 1986)
Solecurtidae	<i>Tagelus</i> , including <i>Tagelus (Meso-pleura)</i> (11)	3.3	<i>Tagelus</i> : semipermanent vertical burrows in mud (Yonge 1955)
			<i>T. plebeius</i> : forms Y-shaped oblique deep permanent burrows that animal can retreat into, in silty fine to very fine sand (Stanley 1970)
			<i>T. divisus</i> : forms Y-shaped burrows in muddy sand (Stanley 1970)
Vesicomysidae	<i>Elenaconcha</i> (1)	4.1 <sup>2</sup>	<i>E. extenta</i> (as <i>Calypptogena extenta</i> ): semi-infaunal in soft sediment at cold seeps at abyssal depths (Sibuet and Olu 1998; Decker et al. 2012)
Veneridae	<i>Petricolaria</i> (7)	3.5 <sup>1</sup>	<i>P. pholadiformis</i> : burrows in soft sediment and bores into rocks (Savazzi 1994); bores into hard clay, mud, peat, wood, or limestone (Zenetos et al. 2009)
Pholadidae	<i>Pholas</i> , including <i>P. (Monothyr)</i> and <i>P. (Thovana)</i> (5)	3.2	<i>Pholas</i> : bore into rocks, coral, wood, and consolidated sediment (Turner 1969; Haga and Kase 2011)
			<i>P. orientalis</i> : deep burrowing in sandy and silty mud (Ronquillo and McKinley 2006)
			<i>Pholas campechiensis</i> : bores into wood, limestone or compacted silts (García-Cubas and Reguero 2007)
Solenidae	<i>Solen</i> , including <i>S. (Neosolen)</i> (67)	5.8	Solenidae: burrows rapidly in sand (Quayle and Newkirk 1989); typically in fine sand within more or less permanent vertical burrows (von Cosel 1990)
	<i>Solena</i> (2)	7.3	



**Table 2.2** (continued)

Family	Genus	L/H	Substrate occurrences and domichnia, if reported in literature
Pharidae	<i>Cultellus</i> (11)	3.3	Pharidae: typically in fine sand within more or less
	<i>Ensiculus</i> (4)	3.4	permanent vertical burrows (von Cosel 1990)
	<i>Ensis</i> (13)	5.4	<i>Ensis</i> : in permanent burrows (Stanley 1970)
	<i>Pharella</i> (7)	4.5	<i>E. directus</i> : typically in cohesive fine sand in per-
	<i>Phaxas</i> (3)	4.1	manent burrows (Stanley 1970)
	<i>Pharus</i> (2)	5.1	<i>Phaxas pellucidus</i> : deep burrower (Chambers 2008)

Length/height (L/H) values are taken from figures illustrated by Moore (1969) unless otherwise indicated by a superscript. Taxonomic placement is based on Carter et al. (2011). The number of species within a genus is listed in parentheses after each genus name and is based on data available in the World Registry of Marine Species (<http://www.marinespecies.org/>)

<sup>1</sup> Huber (2010)

<sup>2</sup> Coan and Valentich-Scott (2012)

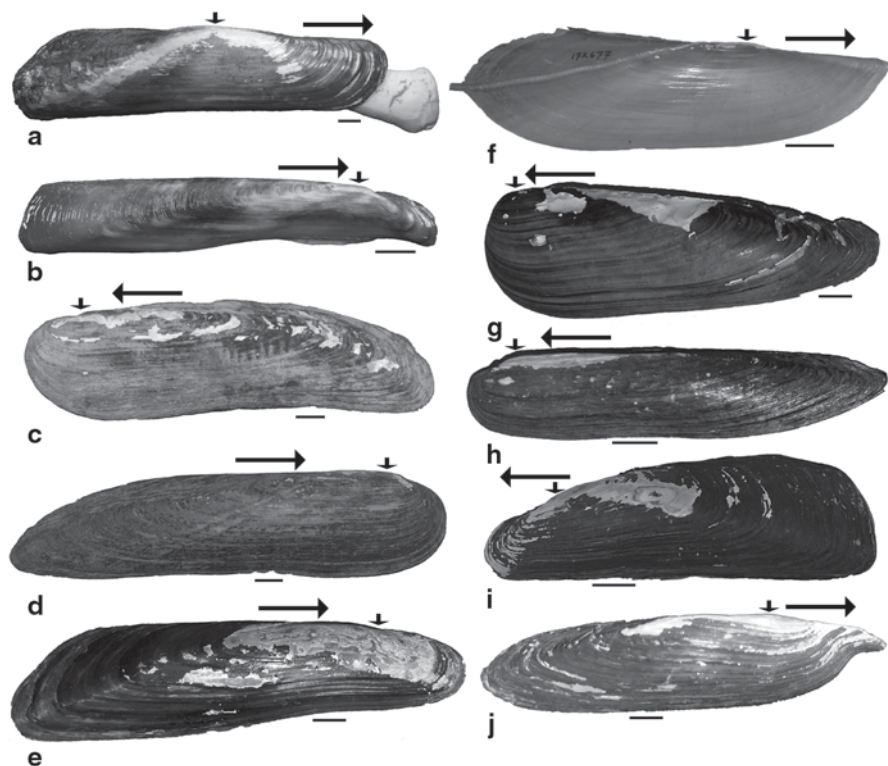
an anterior pedal gape where the two valves do not meet when fully adducted, and through which a long and often cylindrical foot with a dilatable distal end exits the shell (Drew 1907; Yonge 1959; Trueman 1966; Stanley 1970; Bromley and Asgaard 1990; von Cosel 1990; Winter and Hosoi 2011).

Ultra-elongate boring bivalves typically have tubular to cylindrical morphologies with beaks near the valve anterior (<30 % from anterior margin). Examples include *Pholas* (Pholadidae) (Fig. 2.2d), *Petricolaria* (Veneridae) (Fig. 2.2e), *Adula* (Mytilidae) (Fig. 2.2g), and *Lithophaga* (Mytilidae) (Fig. 2.2h). Differences among these taxa include the shape of the ventral margin (concave in *Adula*, convex in *Pholas*, and straight or nearly so in *Petricolaria* and *Lithophaga*), and the position of maximum shell height along the anterior–posterior axis (anterior and at the umbo in *Pholas*, *Petricolaria*, and *Adula*; posterior of the midline in *Lithophaga*). In contrast, *Litharca* (Arcidae) is a uniquely shaped ultra-elongate borer with a cuneiform shell and beak positioned near the posterior of the valve (Fig. 2.2i).

Ultra-elongate species that are nonmotile and epifaunal to semi-infaunal tend to have a curved tubular shell with an anterior beak, as in *Adula* (e.g., species within the mytilids *Gigantidas* or *Adipicola*, and the vesicomysid *Elenaconcha extenta*), or are modioliform (e.g., *Mytella* (Fig. 2.2f) and *Arcuatula*). The ultra-elongate nuculanids (infaunal deposit feeders), *Poroleda* and *Propeleda* retain a nuculanid shape but have greatly extended rostra and relatively low umbos. In contrast, the nuculanid *Adrana* has a nearly straight dorsal margin, anterior and posterior regions that are subequal in shape and length, and a beak located close to the midline.

**2.2.2 Ultra-elongate Unionida**

Ultra-elongate unionoids are distributed across several clades (Fig. 2.1; Table 2.1) and, although shell shape varies among these taxa, many are comparable to particu-



**Fig. 2.3** Examples of ultra-elongate unionoids. Scale bars = 1 cm. *Horizontal arrows* point toward the anterior of each shell. *Vertical arrows* indicate the position of the beak. **a** *Mycetopoda soleniformis* (Río Juruá, Peru). **b** *Mycetopodella falcata* (Río Juruá, Peru). **c** *Elliptio shepardiana* (Altamaha River, Georgia). **d** *Lamproscapha ensiformis* (Brazil). **e** *Solenia iridinea* (China). **f** *Chelidonopsis hirundo* (Democratic Republic of Congo). **g** *Cuneopsis celtiformis* (China). **h** *Lanceolaria grayana* (China). **i** *Lortia rugata* (Australia). **j** *Arconaia lanceolata* (China). Images **a** and **b** are of specimens collected by the author. Image **c** is of a specimen in the Invertebrate Zoology collections of the California Academy of Sciences. Images **d**–**j** were provided by Daniel Graf through the MUSSEL Project (<http://www.mussel-project.net/>) and are of specimens in the Invertebrate Zoology collections of the Smithsonian Institution

lar ultra-elongate marine taxa. For instance, *Mycetopoda soleniformis* (Fig. 2.3a), with its soleniform shape and central beak, resembles an elongate version of *Tagelus* (Fig. 2.2c). In other species of *Mycetopoda*, the shell is more ovate than quadrate and the beak is within 25% of the anterior margin, but is still within the range of shape variation seen in the Pharidae and Solecurtidae (see von Cosel 1990). In addition, like *Tagelus* and razor clams, species of *Mycetopoda* possess an anterior pedal gape through which a long cylindrical foot with a dilated distal end exits the shell (e.g., Fig. 2.3a; see also d'Orbigny 1846; Fischer 1890; Ortmann 1921; Veit-Enheimer and Mansur 1978; Pimpão and Mansur 2009).

The falcate shell with an anterior beak and concave ventral margin of *Mycetopodella* (Fig. 2.3b), and to a lesser extent *Elliptio shepardiana* (Fig. 2.3c), *Lamproscapha* (Fig. 2.3d), and *Lanceolaria* (Fig. 2.3h), resembles that of the boring mytilid *Adula* (Fig. 2.2g). A concave ventral margin is common in mytilids and is associated with byssal attachment along the ventral margin (Stanley 1970, 1972). Unionoids with an *Adula*-like shape, like the similarly shaped vesicomyid *Elenaconcha extenta*, are not byssate as adults. Nonetheless, a relatively large and elongated foot that exits the shell anteroventrally may serve a similar anchoring function at least for *Elenaconcha*, *Mycetopodella*, and *Lamproscapha*. Similarly, the shells of *Solenia iridinea* (Fig. 2.3e) and *Lorttiella rugata* (Fig. 2.3i) resemble the semi-infaunal mytilid *Mytella* in shape (Fig. 2.2f) and, although not byssate, these unionoids also have a large foot that they use for anchorage (Ortmann 1921; Savazzi and Yao 1992).

*Arconaia*, *Chelidonopsis*, and *Cuneopsis* lack marine exemplars. In general outline, *Arconaia* (Fig. 2.3j) resembles *Pholas*, although the former has a shell with a strongly twisted, nonplanar commissure (i.e., has shell torsion) and the latter is characterized by the distinctive hinge, muscle, and accessory plate features of the Pholadidae, rendering the comparison tenuous. The elongate ovate shells of *Chelidonopsis* (Fig. 2.3f) and *Cuneopsis* (Fig. 2.3g) do not closely resemble those of marine ultra-elongate taxa and other distinctive shell features such as pronounced shell torsion (in *Cuneopsis pisciculus* but not *Cuneopsis celtiformis*), or the extremely sharp posteroventral diagonal carinae and posterodorsal margin in *Chelidonopsis hirundo*, may have greater functional relevance for life habit (see Savazzi and Yao 1992).

In summary, the shape of most ultra-elongate unionoids converge on a limited number of exemplar marine taxa, namely razor clams, *Tagelus*, *Adula*, and *Mytella*.

## 2.3 Modes of Differential Shell Growth in Ultra-elongate Bivalves

Distinct modes of differential growth imply diverse developmental pathways for the production of ultra-elongate shapes. To this end, Yonge (1955) used muscle scar shape and beak position to determine patterns of differential growth in ultra-elongate bivalves, including razor clams, *Tagelus*, *Lithophaga*, and *Adula* (as *Botula*), using *Glycymeris* with its central beak and round anterior and posterior adductor scars for comparison. For example, the beak is adjacent to the anterior margin and the anterior adductor scar is elongated in most Pharidae and Solenidae, indicating posterior displacement of the area of maximum shell growth (Yonge 1955) into a region that includes the anterior adductor (Table 2.3; Fig. 2.4a).

By comparison, in *Elenaconcha extenta* (as *Calyptogena extenta*), although the beak is anterior of the midline, neither adductor scar is elongated (see Coan and Valentic-Scott 2012, plate 176), indicating a posterior shift in the center of maximum shell growth that did not affect either adductor. In *Propeleda*, expansion primarily

**Table 2.3** Beak position and shape of adductor muscle scars in extant ultra-elongate bivalves

Adductor scars	Beak $\leq 30\%$ from anterior	Beak 40–50 % from anterior	Beak $> 70\%$ from anterior
Anterior differentially elongated	Pharidae Solenidae		
Both elongated	<i>Pholas</i> <i>Adula</i> <sup>a, b</sup> <i>Lithophaga</i> <sup>a, b</sup>	<i>Adrana</i>	
Posterior differentially elongated	<i>Lortiella</i> <i>Lanceolaria</i> <i>Solenaia</i> <i>Cuneopsis</i> <i>Lamproscapha</i> <i>Arconaia</i> <i>Elliptio shepardiana</i> <i>Mycetopodella</i> <sup>a</sup> <i>Gigantidas</i> <sup>b</sup> <i>Petricolaria</i>	<i>Chelidonopsis</i> <i>Tagelus</i>	
Neither elongate	<i>Elenaconcha extenta</i>  <i>Propeleda</i> <i>Mycetopoda siliquosa</i> <i>Mycetopolda legumen</i> <i>Mytella</i> <sup>a, b</sup>	<i>Mycetopoda soleniformis</i>	<i>Litharca</i>
Muscle scars not observed	<i>Poroleda</i> <i>Adipicola</i> <i>Arcuatula</i>		

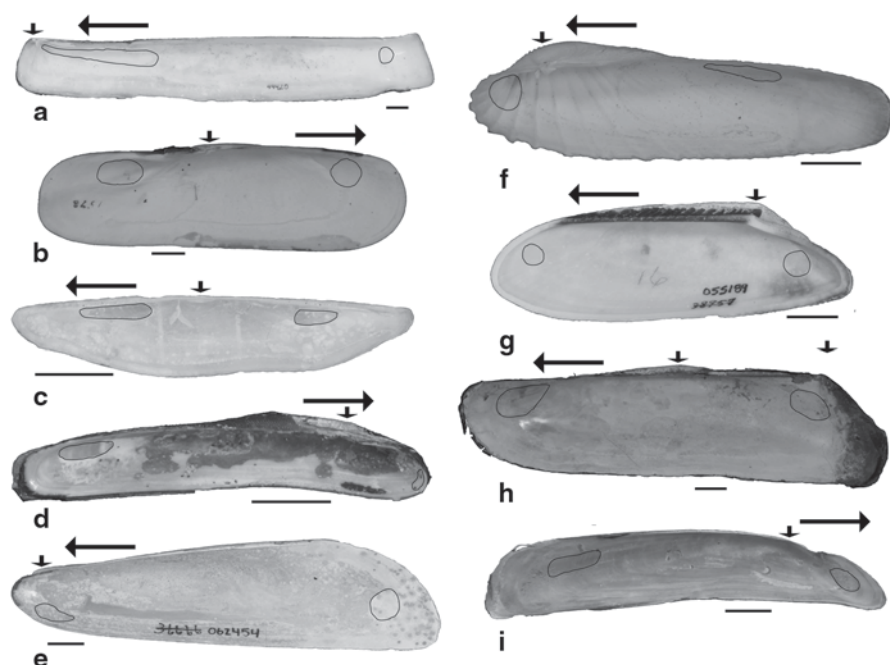
<sup>a</sup> Anterior adductor in an anteroventral position

<sup>b</sup> Elongation accompanied by reduced dorsoventral expansion, particularly of the posterior region of the shell

affects the rostrum posterior of the posterior adductor scar, as this genus retains a nuculanid shape (see McAlester 1969).

In contrast, the beak is central and the posterior adductor scar shows slight elongation in *Tagelus* (Table 2.3; Fig. 2.4b) indicating differential growth both anterior and posterior of the midline, but with only the posterior adductor affected. For the nuculanid *Adrana*, the beak also is central but both adductor scars are elongated (Table 2.3; Fig. 2.4c), indicating that the two growth centers were positioned more distally than in *Tagelus*.

For most ultra-elongate mytilids, elongation is accompanied by a dramatic reduction of dorsoventral height especially in the posterior part of the shell, and as a result the hinge axis has a low oblique angle relative to the anterior–posterior axis (Yonge 1955) (Fig. 2.2f–h). The effect of these proportional changes in growth on muscle scars differs among mytilid taxa. For the boring *Adula* and *Lithophaga*, the adductor scars are elongated compared to the typical heteromyarian state of mytilids, although the anterior adductor retains a characteristic anteroventral position (Fig. 2.4d; see also Yonge 1955). In the *Gigantidas*, in contrast, the posterior scar is



**Fig. 2.4** Beak position and adductor muscle scar shape in various ultra-elongate taxa. Scale bars = 1 cm. Horizontal arrows point toward the anterior of each shell. Vertical arrows indicate the position of the beak. Anterior and posterior adductor muscle scars are outlined. **a** *Solen vagina* (Ireland). **b** *Tagelus californianus* (California). **c** *Adrana scaphoides* (Colombia). **d** *Adula falcata* (California). **e** *Mytella speciosa* (Peru). **f** *Petricolaria pholadiformis* (the Netherlands). **g** *Litharca lithodomus* (Ecuador). **h** *Mycetopoda soleniformis* (Río Juruá, Peru). **i** *Mycetopodella falcata* (Río Juruá, Peru). Images **a–g** are of specimens in the Invertebrate Zoology collections of the California Academy of Sciences. Images **h** and **i** are of specimens collected by the author

elongated and the anterior scar is positioned more dorsally than typical in mytilids (von Cosel and Marshall 2003). *Mytella speciosa*, however, retains unelongated heteromaryian muscle scars (Fig. 2.4e).

In *Pholas* and *Petricolaria*, the beak is positioned near the shell's anterior (Fig. 2.2d, e), and in *Petricolaria* only the posterior adductor scar is elongated, indicating that the maximum area of shell expansion is in the posterior region and incorporates the posterior adductor (Table 2.3; Fig. 2.4f). In *Pholas*, both dorsal adductor scars are elongated (Turner 1969), but the extensively modified musculature and hinge features of this genus make direct comparisons to other bivalves tenuous. In *Litharca*, in contrast to all other ultra-elongate taxa, the beak is near the posterior. Further, although the adductor muscle scars are not elongated, the hinge is extended anteriorly and absent posterior to the beak, indicating anterior placement of the center of maximum shell growth (Table 2.3; Fig. 2.4g).

In most ultra-elongate unionoids, the beak is anteriorly positioned and the posterior adductor scar is elongated (Table 2.3; Fig. 2.4i), in a pattern similar to that

seen in *Petricolaria* (Fig. 2.4f) and *Gigantidas*. This configuration indicates that these ultra-elongate unionoids are posteriorly extended and the maximum area of expansion incorporates the posterior adductor. In *Chelidonopsis*, the central beak and elongated posterior adductor scar imply a pattern of shell expansion similar to *Tagelus* (Fig. 2.4b). *Mycetopoda soleniformis* (Fig. 2.4h) is an exception and has its beak near the shell midline but with neither adductor scar elongated (i.e., elongation pattern similar to *Tagelus* but without posterior adductor scar elongation). For other *Mycetopoda* species, the beak is more anteriorly positioned than in *M. soleniformis*, but like that species, the muscle scars are not elongated (i.e., pattern similar to *Elenaconcha extenta*).

In summary, there are many ways to produce an ultra-elongate shell via differential growth, although for most taxa differential posterior expansion is involved in some manner. In the unionoids, there are primarily four patterns of differential growth (Table 2.3): posterior growth that includes the posterior adductor (in most unionoids), posterior growth that affect neither adductor (in *Mycetopoda siliquosa* and *M. legumen*), both anterior and posterior growth that affects neither adductor (in *Mycetopoda soleniformis*), and both anterior and posterior growth that affects the posterior adductor (*Chelidonopsis hirundo*).

## 2.4 Substrate Preferences and Characteristics of Domichnia in Ultra-elongate Bivalves

Savazzi (1994) in a review of the functional morphology of boring and burrowing invertebrates makes a useful distinction among bivalves that are burrowers (motile in sediment that lacks the strength to support an open burrow), burrow dwellers (form semipermanent burrows in sediment with sufficient strength to support an open burrow), and borers (construct permanent borings in partially lithified deposits, siliciclastic or carbonate rocks, shell, and/or wood). The domichnia (trace fossils that represent dwelling structures) of burrow dwellers and borers form a continuum, with some taxa spanning this range of substrates (e.g., *Petricolaria* and *Pholas*; see Table 2.4).

### 2.4.1 Marine Taxa

Most ultra-elongate marine bivalves are burrow dwellers or borers, including razor clams, *Tagelus*, *Pholas*, *Petricolaria*, *Adula*, *Litharca*, and *Lithophaga* (Table 2.4). That said, several ultra-elongate species within the nuculanids likely are burrowers, based on the family's trophic role as deposit feeders. In addition, several ultra-elongate taxa are sessile epifauna and/or semi-infauna (particularly the byssate mytilids listed in Table 2.4).

Members of the Solenidae, Pharidae, and *Tagelus* are typically reported from relatively cohesive (i.e., can support an open burrow), stable fine-sand substrates



**Table 2.4** Substrate and life modes of extant exemplar ultra-elongate bivalve taxa

Epifaunal to semi-infaunal nonmotile	Burrower in non-cohesive sediment	Burrow dweller in cohesive sediment	Firm ground borer	Hard ground borer
<i>Adipicola</i>	<i>Adrana</i>	<sup>a</sup> <i>Mycetopoda</i>	<i>Adula</i>	<i>Litharca</i>
<i>Arcuatula</i>	<sup>a</sup> <i>Arconaia</i>	<i>legumen</i>	<sup>a</sup> <i>Lortiella rugata</i>	<i>Lithophaga</i>
<i>Elenaconcha</i>	<sup>a</sup> <i>Chelidonopsis</i> (?)	<sup>a</sup> <i>Mycetopoda</i>	<sup>a</sup> <i>Mycetopoda</i>	<i>Petricolaria</i>
<i>Gigantidas</i>	<sup>a</sup> <i>Cuneopsis</i>	<i>siliquosa</i> (?)	<i>soleniformis</i>	<i>Pholas</i>
<i>Mytella</i>	<sup>a</sup> <i>Elliptio shepardiana</i> (?)	<i>Petricolaria</i>	<sup>a</sup> <i>Mycetopodella</i>	
		Pharidae	<i>falcata</i>	
	<sup>a</sup> <i>Lamproscapha</i> (?)	<i>Pholas</i>	<i>Petricolaria</i>	
	<sup>a</sup> <i>Lanceolaria</i>	Solenidae	<i>Pholas</i>	
	<i>Poroleda</i>	<i>Tagelus</i>	<sup>a</sup> <i>Solenaia</i>	
	<i>Propeleda</i>		<i>soleniformis</i>	
	<sup>a</sup> <i>Solenaia iridinea</i>			

For taxa followed by a question mark (?), life habit is inferred from available literature (see Tables 2.1 and 2.2)

<sup>a</sup> = Unionida

(Stanley 1970; Holland and Dean 1977; Quayle and Newkirk 1989; von Cosel 1990). These bivalves are burrow dwellers, and they can quickly descend into their burrows when disturbed (Yonge 1959; Fraser 1967; Stanley 1970; Holland and Dean 1977; von Cosel 1990; also see Drew 1907). When removed from their burrows, however, *Ensis* and *Tagelus* are capable of reburial, often relatively rapidly (Stanley 1970; Winter et al. 2012), unless under physiological distress (Cadée 2000); so they may be considered primarily burrow dwellers and secondarily burrowers because they typically inhabit semipermanent burrows but can also move through soft sediment, particularly when disturbed. The domicinia of solenids and pharids are typically deep and vertical, and are either straight or curved (Yonge 1959; Stanley 1970), whereas in solecurtids burrows are Y-shaped (incurrent and excurrent siphons are unfused and occupy the two arms of the burrow's Y-shaped shafts; Stanley 1970; Holland and Dean 1977; Bromley and Asgaard 1990). The walls of these burrows may be stabilized by compaction and/or by mucus linings (Holland and Dean 1977; Savazzi 1994).

Marine ultra-elongate boring bivalves employ mechanical and/or chemical boring mechanisms. It is generally thought that mechanical boring is more common in poorly lithified siliciclastics and carbonates (here termed firm grounds), whereas chemical boring predominates in well-lithified carbonate rocks (here called hard grounds), bone, and wood. For instance, the mytilid *Adula* is a mechanical borer in mudstones (Yonge 1955; Kleemann 1990, although see Morton 1990), and *Lithophaga* species bore into carbonate rocks, shells, and coral heads by chemical means (Yonge 1955; Kleemann 1990; Morton 1990; Owada 2007), mechanical means (Fang and Shen 1988), or a combination of the two (Appukuttan 2011). Similarly, *Petricolaria* and Pholadidae include both chemical and mechanical borers (Morton 1990; Huber 2010); those taxa (i.e., *Petricolaria*, *Pholas*) that inhabit cohesive

sediment and firm grounds (mud, peat, clay, chalk) use mechanical means of boring (Osler 1826; Duval 1963; Ansell 1970; Haga and Kase 2011; Nederlof and Muller 2012). Boring mechanisms have not been directly investigated in *Litharca*, although Thomas (1976) used morphologic features (weak ligament, reduced anterior pedal retractors, corroded shell exterior) to infer that *Litharca* was a chemical borer, whereas Nicol and Jones (1986) argue that it is a mechanical borer because it is found in sandstones.

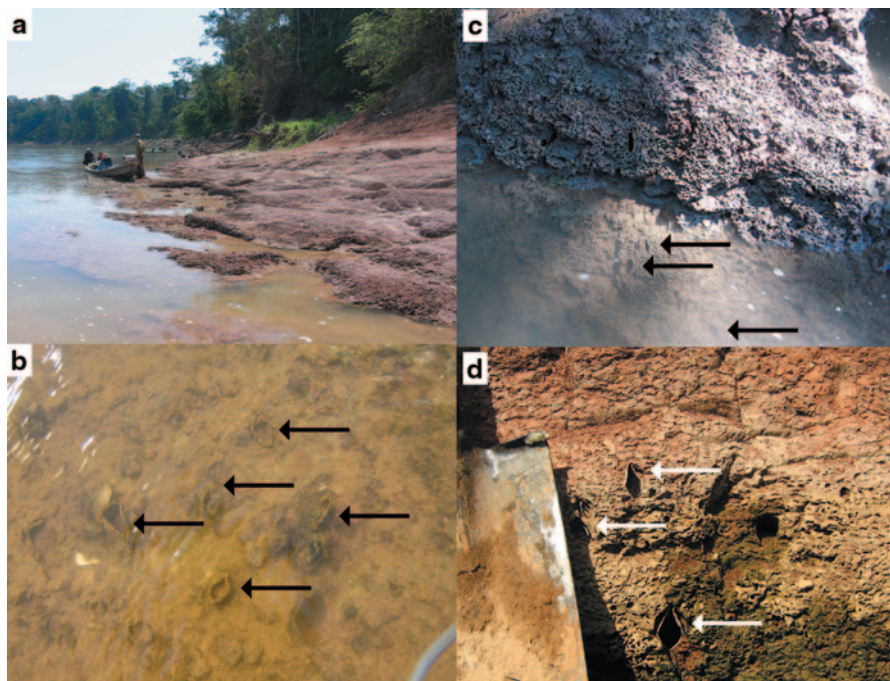
The domichnia of most boring bivalves are perpendicular to the bored surface (Duval 1963; Fankboner 1971; Morton 1990; Pinn et al. 2005) and are comparable to the ichnogenus *Gastrochaenolites*, a flask-shaped boring defined by a straight, narrow neck and larger ovoid chamber in firm to hard substrates (Duval 1963; Kelly and Bromley 1984; Pinn et al. 2005; Hebda 2011; Nederlof and Muller 2012). In contrast to *Gastrochaenolites*, the borings constructed by *Adula* are long and curved (Fankboner 1971). Boring bivalves are typically anchored within their domichnia by a byssus (e.g., *Lithophaga*, *Adula*), with a strong foot (*Pholas*), or by their siphons (*Petricolaria*), and many can retreat into the distal end of their borings and/or contract their siphons when disturbed (Yonge 1955; Nicol and Jones 1986; Savazzi 1994; Pinn et al. 2005; Owada 2007).

#### 2.4.2 *Field Observations of Mycetopodidae in the Upper Amazon Basin (Peru)*

Freshwater ultra-elongate taxa also appear to be distributed across a range of substrates (Table 2.4), including fluvial firm grounds, a setting for which domichnia are minimally documented (although freshwater macroborings are reported in Pleistocene biolithites from Lake Turkana (Ekdale et al. 1989; Lamond and Tapanila 2003) and the Eocene Green River Formation (Lamond and Tapanila 2003)). In an aquatic faunal survey in southeastern Peru, occurrences of the ultra-elongate taxa *Mycetopoda soleniformis* and *Mycetopodella falcata* in fluvial firm grounds were documented (Fig. 2.5). The study area included the Ríos Las Piedras (Madre de Dios drainage), Juruá, and Purús, which drain the Fitzcarrald Arch, a structural/geomorphic feature in southeastern Peru and western Brazil. These rivers are incised, exposing Neogene sediments in some cutbanks (Dumont et al. 1990; Antoine et al. 2007). Where incision reaches well-consolidated clays, these sediments typically form the local base level and are exposed at and below the average dry-season water level in cutbanks and rapids (Campbell et al. 2010) (Fig. 2.5a).

*Mycetopoda soleniformis* and *Mycetopodella falcata* typically occur sympatrically below the average dry-season water level in cutbank exposures of semilithified muds and within rapids associated with similar semilithified subaqueous outcrops in the main channels of the Ríos Purús, Juruá, and Las Piedras (Fig. 2.5). Another unionoid, *Bartlettia stefanensis* (Etheriidae), also occurs but rather than boring, it wedges its posterior into crevices within these firm grounds. Burmeister (1988) reports similar cooccurrences of *Mycetopoda soleniformis*, *Mycetopodella falcata*,





**Fig. 2.5** Firm grounds in incised river channels of the Fitzcarrald Arch. Arrows indicate *Mycetopoda soleniformis* borings. **a** partially exposed firm ground at average dry season low water level in the Río Purús; **b** firm ground surface with dead *Mycetopoda soleniformis* partially exposed within their borings, Río Jurúa; **c** surface of firm ground showing complex boring patterns in substrate, Río Purús; **d** partially weathered firm ground surface with dead *Mycetopoda soleniformis* within their borings, Río Jurúa

and *B. stefanensis* in “hard laterites” along the banks of the Río Yuyapichis (= Yuya Pichis or Lullapichis), Peru.

The areas colonized by these unionoids possess trace assemblages similar to those in *Glossifungites* or *Trypanites* ichnofacies with much of the firm ground surface riddled with small borings made by larval insects (Fig. 2.5c, d). The borings that *M. soleniformis* and *M. falcata* excavate are roughly perpendicular to the outcrop surface below the average dry-season water line and outside of areas that experience high bedload sediment transport and deposition. *Mycetopoda soleniformis* constructs an ovate, smooth-sided boring (slightly wider and ~1.5 times longer than its body), into which it can retreat using rapid pedal–muscle retraction while strongly anchoring itself with the foot’s bulbous end (d’Orbigny 1846; Veitenheimer and Mansur 1978; pers. obs.) (Fig. 2.5b–d). d’Orbigny (1846) compares the “manner of living” of *Mycetopoda* (as *Mycetopus*) to that of pholads boring into stone and infers that members of the genus bore by mechanical means.

*Mycetopodella falcata* does not have as strong an anchorable foot as *Mycetopoda*, although Marshall (1927) suggests that its falcate-shaped shell provides anchor-

age. *Mycetopodella* can be extracted from its boring with relative ease, however, because their burrows are only slightly longer than the shell's length so they cannot retreat as deeply into the substrate and their foot provides little resistance when pulled from their burrows.

For other mycetopodids, *Mycetopoda legumen* forms more or less permanent burrows in compacted sand (Veitenheimer and Mansur 1978), *M. siliquosa* occurs in muds (d'Orbigny 1846; Castillo et al. 2007; Pimpão et al. 2008) and unconsolidated sand (pers. obs.), and *Lamproscapha ensiformis* is reported from within a large channel-bar complex at the confluence of Rios Negro, Amazonas, and Solimões in Brazil (Pimpão et al. 2008). For the latter two species, it is not clear from the literature whether they are burrowers or burrow dwellers.

### 2.4.3 Other Ultra-elongate Unionoids

Other ultra-elongate unionoids also are firm ground dwellers. *Lortia rugata* is reported from under rocks, among tree roots in mud, and in tube-like burrows in mudbanks in coastal rivers of northwestern Australia (Lamprell and Healy 1998; Ponder and Bayer 2004). Based on the locality description in Ponder and Bayer (2004), the "mudbanks" are likely firm grounds, and *L. rugata* excavate domicinia that they retreat into when the animals are disturbed. Similarly, *Solenia soleniformis* (as *Balwantia*) is reported as occupying permanent burrows/borings in firm ground clays below seasonal low water in India (Annandale 1919; Godwin-Austen 1919; Prashad 1919). Annandale (1919) infers that this species is a mechanical borer, and Ortmann (1921) and Fischer (1890) note that the foot of *Solenia* is like that of *Mycetopoda* (long with a dilated distal end), and that these bivalves retreat into their boreholes when disturbed.

Ultra-elongate unionoids are not limited to firm grounds, however. *Cuneopsis celtiformis*, *C. pisciculus*, and *Lanceolaria grayana*, were collected by Savazzi and Yao (1992) in well-oxygenated lake sediments and river channels. Based on subsequent aquarium observations, the authors considered these taxa active burrowers. Savazzi and Yao (1992) also reported that these taxa, as well as *Arconaia lanceolata*, are oriented subhorizontally when in life position in aquaria. Unlike *Cuneopsis* and *Lanceolaria*, *A. lanceolata* was collected from soft, methane-rich, anoxic lake muds with *Solenia iridinea* (as *S. oleivora*). In fact, Savazzi and Yao (1992) infer that the latter two species may be chemosymbiotic due to their environmental occurrence and features such as a nonretractable, sulfur-yellow foot in *S. iridinea* and an anterior rostrum in *A. lanceolata*.

*Chelidonopsis hirundo*, which is endemic to the Congo Basin (Mandahl-Barth 1988), is reported from sandy and gravelly bottoms just below or above rocky barriers (Pilsbry and Bequaert 1927). It is not clear from these descriptions whether *Chelidonopsis* is a burrower or a burrow dweller. Similarly, the North American *Elliptio shepardiana* is reported from stable protected river banks in fine sand and silt behind roots and around logs and trees (University of Georgia Museum of Natural History 1996), and it is not clear whether this species is a burrower or a burrow dweller.

## 2.5 Discussion

Investigations of adaptation and constraint have an important history in both paleontological and neontological literature, with renewed interest as mechanisms of evolutionary developmental biology have been elucidated (e.g., Shubin et al. 2009; Futuyma 2010; Losos 2011; McGhee 2011; Wake et al. 2011). In this context, morphologic convergence is of particular interest because it may be interpreted on a continuum from “natural selection produces an optimal solution for a given set of environmental conditions” to “constraints limit available variation so that a given morphology is inevitable” (Thomas 1978a, 1988; Wake 1999; Brakefield and Roskam 2006; McGhee 2011; Losos 2011). Distinguishing where on that continuum a potential modern analog falls is valuable in understanding its limits as a reliable proxy for the fossil record.

Bivalves as a whole and clades within this class have been the focus of numerous studies examining the roles of adaptation and constraint in morphologic evolution (e.g., Stanley 1975; Thomas 1976, 1978a, b, 1988; Seilacher 1984; Savazzi 1987; Harper and Skelton 1993; Ubukata 2000; Anderson and Roopnarine 2005; Goodwin et al. 2008; Alejandrino et al. 2011). In general, traits such as gill form and function, shell microstructure, hinge features (ligament, dentition), and spiral shell growth are viewed as constrained, whereas shell shape and ornament are less refractory (Stanley 1975; Thomas 1978a, b, 1988; Seilacher 1984; Checa and Jiménez-Jiménez 2003; Serb et al. 2011). Interpretations of shell shape in bivalves, especially marine bivalves, typically focus on functional (adaptive) inference related to substrate preferences and life habit (e.g., Stanley 1970; Seilacher 1984; Thomas 1978a, 1988; Alejandrino et al. 2011). Ultra-elongate shell shapes as convergent forms occurring in multiple clades would, therefore, seem compelling as potential environmental indicators.

Ultra-elongate morphologies, however, occur across multiple substrates and life habits (Table 2.4). In other words, these convergences do not have simple relationships with the factors typically thought to be important selective agents on shell shape. Even comparing bivalves with similar overall shapes (e.g., *Mytella* as a semi-infaunal byssate taxon vs. *Lortia rugata* as a firm ground dweller) and/or similar modes of elongation (e.g., *Tagelus* as a burrow-dweller vs. *Mycetopoda soleniformis* as a firm ground borer), reveal a diversity of life modes and substrate preferences. As a consequence, ultra-elongate morphologies either are not reliable environmental proxies because shell shape is not strongly controlled by factors such as substrate type and life habit, or is indicative of a factor common across substrates and life habits.

Deeming ultra-elongate shapes as environmentally uninformative runs counter to much previous work on bivalve functional morphology. For infaunal motile bivalves especially, the shell plays a critical role as an anchor during the burrowing cycle, but also is a resistant body part that must be pulled through the sediment, implying that functional factors strongly influence shell morphology (Stanley 1970; Seilacher 1984; Savazzi 1994). This does not mean, however, that all infaunal bivalves have the same shape, and in fact most are not ultra-elongate. In addition,

differences in burrowing style related to differences in shell shape and ornamentation have been previously reported. For instance, clams such as *Mercenaria* incorporate an anterior/posterior rocking motion when burrowing, and rely on both shell sculpture and their prosogyrous anteriors to slice through the sediment and penetrate downward (Stanley 1975; Savazzi 1994). Some unionoids that are not ultra-elongate burrower in a similar way (Savazzi and Yao 1992).

In contrast, bivalves with ultra-elongate shells tend to burrow via direct penetration (i.e., without anterior/posterior shell rotation) and the small anterior cross-sectional area of the shell provides relatively low resistance as they move through the sediment (Stanley 1970, 1975). In fact, *Ensis directus* serves as a biological model for burrowing and retractable-anchor technologies, because of its ability to burrow efficiently (energy scales linearly with depth rather than by depth<sup>2</sup>) and rapidly (Winter and Hosoi 2011; Winter et al. 2012). This type of burrowing has been described for Pharidae, Solenidae, *Tagelus*, *Petricolaria pholadiformis*, and the unionoid *Lanceolaria grayana* (Stanley 1970; von Cosel 1990; Savazzi and Yao 1992; Savazzi 1994; Winter and Hosoi 2011). The unionoid *Cuneopsis* serves as an exception to this association of direct penetration burrowing and an ultra-elongate morphology; *C. celtiformis* and *C. pisciculus* are reported to rock back and forth within the commissural plane while burrowing (Savazzi and Yao 1992). Members of this genus, however, tend to have an inflated anterior relative to other ultra-elongate taxa (Fig. 2.3g), which might explain differing burrowing behaviors.

Most boring ultra-elongate bivalves also have cylindrical forms, again providing a small cross-sectional area in the direction of penetration. In addition, for mechanical borers (pholads, *Petricolaria*, *Mycetopoda*, *Solenia*), substrate penetration is accomplished in a similar manner to that of burrowing ultra-elongate bivalves (d'Orbigny 1846; Annandale 1919; Yonge 1955; Ansell 1970; Savazzi 1994, 1999; Haga and Kase 2011; pers. obs.), although shell ornament (ridges, teeth) in pholads and *Petricolaria* also plays a role in the boring process (Morton 1990; Savazzi 1994, 1999).

Therefore, instead of dismissing ultra-elongate morphologies as uninformative, it may be that this shape reflects the way a substrate is penetrated (i.e., direct penetration without major anterior/posterior rotation), rather than the type of substrate penetrated. In other words, the ultra-elongate shape reflects a set of behaviors rather than a particular substrate or life habit. Constructing this functional/behavioral hypothesis to explain ultra-elongate shell shapes does not rule out a role for constraint in producing these morphologies but, given that an ultra-elongate shape can be achieved through a variety of differential growth pathways (Table 2.3), it seems that its role is at most a minor one.

There are exceptions to this association between ultra-elongate shape and direct penetration of substrates. Examples include ultra-elongate epifaunal to semi-infaunal byssate mytilids, and may also include ultra-elongate unionoids that burrow in noncohesive sediments (Savazzi 1994). In these cases, an ultra-elongate shape may serve a different purpose, be an epiphenomenon, or may require additional data to be tested. For instance, in the epi- and semi-infaunal mytilids and the vesi-

comiid *Elenaconcha extenta*, an elongate shape may enhance anchorage (Stanley 1972). For the unionoids, it may be in part that substrate preferences, life habit, and burrowing behaviors are insufficiently documented to be tested. Savazzi and Yao (1992) noted, however, that in aquaria: (1) *Cuneopsis* spp. uses an anterior/posterior rocking motion during burrowing; (2) the resting position of *Cuneopsis* spp., *Lanceolaria grayana*, and *Arconaia lanceolata* is subhorizontal; and (3) unlike many marine ultra-elongates, the shells of *A. lanceolata* and *C. pisciculus* exhibit pronounced torsion. Marine bivalves with shell torsion tend to be nonsiphonate endobysate taxa that position the posterior portion of the commissure parallel with the sediment/water interface, presumably to increase the surface area of the mantle in contact with the water column (Tevesz and Carter 1979; Seilacher 1984; Savazzi 1989; Savazzi and Yao 1992). Although unionoids are not byssate, the function of shell torsion may be similar, providing anchorage while maximizing the mantle's contact with the water column (Savazzi and Yao 1992). Similarly, *L. grayana* and *C. celtiformis*, although without torsion, show a low angle of penetration into the sediment and position themselves with their ventral margin at the sediment/water interface (Savazzi and Yao 1992). In other words, an elongate shape also may serve as a way to maximize mantle area exposure to the water column in nonsiphonate bivalves.

## 2.6 Conclusions

Although convergence upon an ultra-elongate shape occurs in bivalves that inhabit a range of substrates and with a variety of life habits, constraints likely are not strongly canalizing morphology, as ultra-elongate shapes are achieved through a variety of pathways of differential shell elongation. Instead, for many taxa an ultra-elongate shape primarily reflects a set of behaviors used in penetrating any substrate rather than particular types of substrate or life habits. Additional morphologic, ecologic, and behavior studies, particularly under natural conditions, for both marine and unionoid taxa could test this hypothesis. Refining modern analogs with such knowledge is useful not only in interpreting the fossil record, but also for informing efforts to protect and restore extinction-prone extant species of unionoids.

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## References

- Alejandrino A, Puslednik L, Serb JM (2011) Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). BMC Evol Biol 11:164. doi:10.1186/1471-2148-11-164
- Anderson LC, Roopnarine PD (2005) Role of constraint and selection in the morphologic evolution of *Caryocorbula* (Mollusca: Corbulidae) from the Caribbean Neogene. Palaeontol Electron 8(2):32A
- Annandale N (1919) Further notes on the burrows of *Solenia soleniformis*. Rec Indian Mus 16:205–206
- Ansell AD (1970) Boring and burrowing mechanisms in *Petricola pholadiformis* Lamarck. J Exp Mar Biol Ecol 4:211–220
- Antoine P-O, Salas-Gismondi RS, Baby P, Benammi M, Brusset S, de Franceschi D, Espurt N, Goillot C, Pujos F, Tejada J, Urbina M (2007) The Middle Miocene (Laventan) Fitzcarrald fauna, Amazonian Peru. In: Díaz-Martínez E, Rábano I (eds) 4th European meeting on the palaeontology and stratigraphy of Latin America. Cuadernos del Museo Geominero. Instituto Geológico y Minero de España, Madrid, pp 19–24
- Appukuttan KK (2011) On *Lithophaga (Diberus) bisulcata* a mytilid borer causing damage to the commercially important gastropod shells. Indian J Fish 23:194–200
- Bieler R, Carter JG, Coan EV (2010) Classification of bivalve families. In: Bouchet P, Rocroi J-P (eds) Nomenclator of bivalve families. Malacologia 52:113–184
- Bogan AE (1993) Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. Am Zool 33:599–609
- Bogan A, Bouchet P (1998) Cementation in the freshwater bivalve family Corbiculidae (Mollusca: Bivalvia): a new genus and species from Lake Poso, Indonesia. Hydrobiologia 389:131–139
- Bogan AE, Roe K (2008) Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future directions. J N Am Benthol Soc 27:349–369
- Brakefield PM (2006) Evo-devo and constraints on selection. Trends Ecol Evol 21:362–368
- Brakefield PM, Roskam JC (2006) Exploring evolutionary constraints is a task for an integrative evolutionary biology. Am Nat 168(Supplement):S1–S13
- Bromley RG, Asgaard U (1990) *Solecurtus strigilatus*: a jet-propelled burrowing bivalve. In: Morton B (ed) The Bivalvia—proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge. Hong Kong University Press, Hong Kong, pp 313–320
- Burmeister E-G (1988) Beobachtungen zur Lebensweise von *Bartlettia stefanensis* (Moricand, 1856) am Rio Llullapichis (Peru) (Mollusca, Eulamellibranchia). Spixiana 11:27–36
- Cadée GC (2000) Herring gulls feeding on a recent invader in the Wadden Sea, *Ensis directus*. In: Harper EM, Taylor JD, Crame JA (eds) Evolutionary biology of the Bivalvia. The Geological Society, Bath, pp 459–464
- Campbell DC, Lydeard C (2012) The genera of Pleurobemini (Bivalvia: Unionidae: Ambleminae). Am Malacol Bull 30:19–38
- Campbell KE Jr, Prothero DR, Romero-Pittman L, Hertel F, Rivera N (2010) Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. J S Am Earth Sci 29:619–626
- Carter JG, Altaba CR, Anderson LC, Araujo R, Biakov AS, Bogan AE, Campbell DC, Campbell M, Jin-hua C, Cope JCW, Delvene G, Dijkstra HH, Zong-jie F, Gardner RN, GavriloVA, Goncharova IA, Harries PJ, Hartman JH, Hautmann M, Hoeh WR, Hylleberg J, Bao-yu J, Johnston P, Kirkendale L, Kleemann K, Koppka J, Kříž J, Machado D, Malchus N, Márquez-Alíaga A, Masse J-P, McRoberts CA, Middelfart PU, Mitchell S, Nevesskaja LA, Özer S, Pojeta JJ, Polubotko IV, Pons JM, Popov S, Sánchez T, Sartori AF, Scott RW, Sey II, Signorelli JH, Silantiev VV, Skelton PW, Steuber T, Waterhouse JB, Wingard GL, Yancey T (2011) A synoptical classification of the Bivalvia (Mollusca). Paleontol Contrib 4:1–47
- Castillo AR, Brasil LG, Querol E, Querol MVM, Oliveira EV, Mansur MCD (2007) Moluscos bivalves da localidade de São Marcos, bacia do Médio rio Uruguai, Uruguaiana, Brasil. Biotemas 20:73–79

- Chambers P (2008) Channel Island marine molluscs: an illustrated guide to the seashells of Jersey, Guernsey, Alderney, Sark and Herm. Charonia Media
- Checa AG, Jiménez-Jiménez AP (2003) Rib fabrication in Ostreoida and Plicatuloidea (Bivalvia, Pteriomorphia) and its evolutionary significance. *Zoomorphology* 122:145–159
- Coan EV, Valentich-Scott P (2012) Bivalve seashells of tropical Western America marine bivalve mollusks from Baja California to northern Perú. Santa Barbara Museum of Natural History, Santa Barbara
- Cubo J (2004) Pattern and process in constructional morphology. *Evol Dev* 6:131–133
- Dautzenberg P, Fischer H (1905) Liste des mollusques récoltés par M. le Capitaine de Frégate Blaise au Tonkin, et description d'espèces nouvelles. *J Conch Paris* 53:85–234
- d'Orbigny A (1846) Voyage dans l'Amérique Méridionale (le Brésil, la République de Orientale de l'Uruguay, la République Argentine, la Patagonie, République du Chili, la République de Bolivie, la République de Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Tome 5, Partie 3, Mollusques. Pitois-Levrault, Strasbourg
- Decker C, Olu K, Cunha RL, Arnaud-Haond S (2012) Phylogeny and diversification patterns among vesicomyid bivalves. *PLoS ONE* 7:e33359. doi:10.1371/journal.pone.0033359
- Drew GA (1907) The habits and movements of the razor-shell clam, *Ensis directus*. *Biol Bull* 12:127–140
- Dumont JF, Lamotte S, Kahn F (1990) Wetland and upland forest ecosystems in Peruvian Amazonia: plant species diversity in the light of some geological and botanical evidence. *Forest Ecol Manag* 33/34:125–139
- Duval DM (1963) The biology of *Petricola pholadiformis* Lamarck (Lamellibranchiata Petricolidae). *Proc Malacol Soc Lond* 35:89–100
- Ekdale AA, Brown FH, Feibel CS (1989) Nonmarine macroborings in early Pleistocene algal biolithites (stromatolites) of the Turkana Basin, Northern Kenya. *Palaios* 4:389–396
- Fang L-S, Shen P (1988) A living mechanical file: the burrowing mechanism of the coral-boring bivalve *Lithophaga nigra*. *Mar Biol* 97:349–354
- Fankboner PV (1971) The ciliary currents associated with feeding, digestion, and sediment removal in *Adula (Botula) falcata* Gould 1851. *Biol Bull* 140:28–45
- Fischer P (1890) Observations sur les genres *Mycetopus* et *Solenia*. *J Conch Paris Series* 3(30):5–14
- Fraser TH (1967) Contributions to the biology of *Tagelus divisus* (Tellinacea: Pelecypoda) in Biscayne Bay, Florida. *B Mar Sci* 17:111–132
- Futuyma DJ (2010) Evolutionary constraint and ecological consequences. *Evolution Int J org Evolution* 64:1865–1884. doi:10.1111/j.1558-5646.2010.00960.x
- García-Cubas A, Reguero M (2007) Catalogo ilustrado de moluscos bivalvos del Golfo de México y Mar Caribe. UNAM, Instituto de Ciencias del Mar y Limnología, México
- Godwin-Austen HH (1919) Description of a new species of *Margaritanopsis* (Unionidae) from the southern Shan States, with notes on *Solenia soleniformis*. *Rec Indian Mus* 16:203–205, pl. 215
- Goodwin DH, Anderson LC, Roopnarine PD (2008) Evolutionary origins of novel conchologic growth patterns in tropical American corbulid bivalves. *Evol Dev* 10:642–656
- Gould SJ (2002) The structure of evolutionary theory. The Belknap Press of Harvard University Press, Cambridge
- Graf DL (2013) Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoida, Sphaeriidae, and Cyrenidae. *Am Malacol Bull* 31:135–153
- Graf DL, Cummings KS (2006) Palaeoheterodont diversity (Mollusca: Trigonioida + Unionoida): what we know and what we wish we knew about freshwater mussel evolution. *Zool J Linn Soc-Lond* 148:343–394
- Graf DL, Cummings KS (2007) Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *J Mollus Stud* 73:291–314
- Grove SJ (2011) A guide to the seashells and other marine molluscs of Tasmania <http://www.molluscosoftasmania.net>. Accessed 21 Aug 2012

- Haag WR (2012) North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, Cambridge
- Haas F (1969) Superfamily Unionacea Fleming, 1828. In: Moore RC (ed) Treatise on invertebrate paleontology, part N, volume 1, Mollusca 6 Bivalvia. The University of Kansas and the Geological Society of America, Inc., Boulder, pp 411–467
- Haga T, Kase T (2011) *Opertochasma somaensis* n. sp. (Bivalvia: Pholadidae) from the Upper Jurassic in Japan: a perspective on pholadoidean early evolution. *J Paleontol* 85:478–488
- Harper EM, Skelton PW (1993) The Mesozoic marine revolution and epifaunal bivalves. *Scripta Geol Spec Issue* 2:127–153
- Hashimoto J, Yamane T (2005) A new species of *Gigantidas* (Bivalvia: Mytilidae) from a vent site on the Kaikata Seamount southwest of the Ogasawara (Bonin) Islands, Southern Japan. *Venus: Jap J Malacol* 64:1–10
- Hebda A (2011) Information in support of a recovery potential assessment of Atlantic mud-piddock (*Barnea truncata*) in Canada. DFO Canadian Science Advisory Secretariat Research Document 2010/117:30 p
- Holland AF, Dean JM (1977) The biology of the stout razor clam *Tagelus plebeius*: I. Animal-sediment relationships, feeding mechanism, and community biology. *Chesap Sci* 18:58–66
- Huang Y, Liu H, Wu X, Ouyang S (2002) Testing the relationships of Chinese freshwater Unionidae (Bivalvia) based on analysis of partial mitochondrial 16S rRNA sequences. *J Mollus Stud* 68:359–363
- Huber M (2010) Compendium of bivalves. ConchBooks, Hackenheim
- Kelly RA, Bromley RG (1984) Ichneological nomenclature of clavate borings. *Palaeontology* 27:793–807
- Kleemann K (1990) Evolution of chemically-boring Mytilidae (Bivalvia). In: Morton B (ed) The Bivalvia—proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge. Hong Kong University Press, Hong Kong, pp 111–124
- Kyuno A, Shintaku M, Fujita Y, Matsumoto H, Utsumi M, Watanabe H, Fujiwara Y, Miyazaki J-I (2009) Dispersal and differentiation of deep-sea mussels of the genus *Bathymodiolus* (Mytilidae, Bathymodiolinae). *J Mar Biol* 2009:1–15. doi:10.1155/2009/625672
- Lamond RE, Tapanila L (2003) Embedment cavities in lacustrine stromatolites: evidence of animal interactions from Cenozoic carbonates in U.S.A. and Kenya. *Palaios* 18:445–453
- Lamprell K, Healy J (1998) Bivalves of Australia, vol 2. Backhuys Publishers, Leiden
- Lorion J, Duperron S, Gros O, Cruaud C, Samadi S (2009) Several deep-sea mussels and their associated symbionts are able to live both on wood and on whale falls. *P Roy Soc B* 276:177–185. doi:10.1098/rspb.2008.1101
- Losos JB (2011) Convergence, adaptation, and constraint. *Evolution Int J org Evolution* 65:1827–1840. doi:10.1111/j.1558-5646.2011.01289.x
- Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of nonmarine mollusks. *Bioscience* 54:321–330
- Mandahl-Barth G (1988) Studies in African freshwater bivalves. Danish Bilharziasis Laboratory, Charlottendlund
- Mansur MCD, dos Santos CP, Darrigran G, Heydrich I, Callil CT, Cardoso FR (2003) Primeiros dados quali-quantitativos do mexilhão-dourado, *Limnoperna fortunei* (Dunker), no Delta do Jacuí, no Lago Guaíba e na Laguna dos Patos, Rio Grande do Sul, Brasil e alguns aspectos de sua invasão no novo ambiente. *Rev Bras Zool* 20:75–84
- Marshall WB (1927) A new genus and two new species of South American fresh-water mussels. *Proc US Natl Mus* 71:10–12
- McAlester AL (1969) Superfamily Nuculanacea H. Adams & A. Adams, 1858. In: Moore RC (ed) Treatise on invertebrate paleontology, part N, volume 1, Mollusca 6 Bivalvia. The University of Kansas and the Geological Society of America, Inc., Boulder, pp 231–235
- McGhee GR Jr (2011) Convergent evolution: limited forms most beautiful. The MIT Press, Cambridge



- Moore RC (1969) Treatise on invertebrate paleontology, part N, volume 1–2, Mollusca 6 Bivalvia. The University of Kansas and The Geological Society of America, Inc., Boulder
- Morton B (1990) Corals and their bivalve borers—the evolution of a symbiosis. In: Morton B (ed) The Bivalvia—proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge. Hong Kong University Press, Hong Kong, pp 11–45
- Nederlof R, Muller M (2012) A biomechanical model of rock drilling in the piddock *Barnea candida* (Bivalvia; Mollusca). J R Soc Interface 7(76):12 p. doi:10.1098/rsif.2012.0329
- Nicol D, Jones DS (1986) *Litharca lithodomus* and adaptive radiation in arcacean pelecypods. Nautilus 100:105–110
- Nijssen-Meyer J (1972) *Propeleda platessa* (Dall, 1890), a nut clam new for the coastal waters of Surinam (Pelecypoda, Nuculanidae). Zool Med Leiden 47:449–456
- Ortmann AE (1921) South American naiades; a contribution to the knowledge of the freshwater mussels of South America. Mem Carnegie Mus 8:451–670, pls.434–448
- Osler E (1826) On burrowing and boring marine animals. Philos T R Soc Lon 116:342–371
- Ouyang J, We X, Ouyang S, Li S, Zhao D (2011) Phylogenetic analysis of some Chinese freshwater Unionidae based on mitochondrial COI sequences. J Conchol 40:543–548
- Owada M (2007) Functional morphology and phylogeny of the rock-boring bivalves *Leiosolenus* and *Lithophaga* (Bivalvia: Mytilidae): a third functional clade. Mar Biol 150:853–860
- Pilsbry HA, Bequaert J (1927) The aquatic mollusks of the Belgian Congo. With a geographical and ecological account of Congo malacology, with field notes by the collectors, H. Land and J.P. Chapin. B Am Mus Nat Hist 53:69–602, pls. 610–677
- Pimpão DM, Mansur MCD (2009) Chave pictória para identificação dos bivalves do baixo Rio Aripuanã, Amazonas, Brasil (Sphaeriidae, Hyriidae e Mycetopodidae). Biota Neotrop 9:377–384
- Pimpão DM, Rocha MS, de Caastro Fettuccia D (2008) Freshwater mussels of Catalão, confluence of Solimões and Negro Rivers, State of Amazonas, Brazil. Check List 4:395–400
- Pinn EH, Richardson CA, Thompson RC, Hawkins SJ (2005) Burrow morphology, biometry, age and growth of piddocks (Mollusca: Bivalvia: Pholadidae) on the south coast of England. Mar Biol 147:943–953
- Ponder WF, Bayer M (2004) A new species of *Lortietta* (Mollusca: Bivalvia: Unionoidea: Hyriidae) from northern Australia. Molluscan Res 24:89–102
- Powell AWB (1979) New Zealand Mollusca: marine, land and freshwater shells. Collins, Auckland
- Prashad B (1919) XIX. Studies on the anatomy of Indian Mollusca. 3. The soft parts of some Indian Unionidae. Rec Indian Mus 16:289–296
- Quayle DB, Newkirk GF (1989) Farming bivalve molluscs: methods for study and development. Advances in world aquaculture, vol 1. Louisiana State University, Baton Rouge
- Ríos-Jara E, Navarro-Caravantes CM, Galván-Villa C-M, Lopez-Uriarte E (2009) Bivalves and gastropods of the Gulf of Tehuantepec, Mexico: a checklist of species with notes on their habitat and local distribution. J Mar Biol. 2009: 12 p. doi:10-1155/2009/176801
- Ronquillo JD, McKinley RS (2006) Developmental stages and potential mariculture for coastal rehabilitation of endangered Pacific angelwing clam, *Pholas orientalis*. Aquaculture 256:180–191
- Saavedra L, Dornelles LMA, Santos SB, Absalão R, Anjos SMC, Melo GV, Stanton NSG, Fonseca EM, Lima LL, Küsel ET, Ribeiro EO, Lazillota AAA, Esteves FA (1999) Caracterização oceanográfica da plataforma continental interna adjacente ao Cabo Frio—RJ, no Inverno de 1995. Oecologia Aust 7:245–272
- Santos HSS, Beasley CR, Tagliaro CH (2010) Changes in population characteristics of *Mytella falcata* (d'Orbigny, 1846) beds, an exploited tropical estuarine mussel. Bol Inst Pesca 36:85–97
- Savazzi E (1987) Geometric and functional constraints on bivalve shell morphology. Lethaia 20:293–306
- Savazzi E (1989) Shell torsion and life habit in the recent mytilid bivalve *Modiolus philippinarum*. Palaeogeogr Palaeoclimatol 72:277–282
- Savazzi E (1994) Functional morphology of boring and burrowing invertebrates. In: Donovan SK (ed) The palaeobiology of trace fossils. The Johns Hopkins University Press, Baltimore, pp 43–82

- Savazzi E (1999) Boring, nestling and tube-dwelling bivalves. In: Savazzi E (ed) *Functional morphology of the invertebrate skeleton*. Wiley, Chichester, pp 205–237
- Savazzi E, Yao P (1992) Some morphological adaptations in freshwater bivalves. *Lethaia* 25:195–209
- Schwenk K, Wagner GP (2004) The relativism of constraints on phenotypic evolution. In: Pigliucci M, Preston K (eds) *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford University Press, Oxford, pp 390–408
- Seilacher A (1984) Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* 27:207–237
- Serb JM, Alejandrino A, Otárola-Castillo E, Adams DC (2011) Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae). *Zool J Linn Soc-Lond* 163(2):571–584. doi:10.1111/j.1096-3642.2011.00707.x
- Shubin N, Tabin C, Carroll S (2009) Deep homology and the origins of evolutionary novelty. *Nature* 457:818–823. doi:10.1038/nature07891
- Sibuet M, Olu K (1998) Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Res Pt II* 45:517–567
- Stanley SM (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). *Geo Soc Mem* 125:1–296
- Stanley SM (1972) Functional morphology and evolution of byssally attached bivalve mollusks. *J Paleontol* 46:165–212
- Stanley SM (1975) Adaptive themes in the evolution of the Bivalvia (Mollusca). *Annu Rev Earth Pl Sci* 3:361–385
- Tevesz MJS, Carter JG (1979) Form and function in *Trisidos* (Bivalvia) and a comparison with other burrowing arcoids. *Malacologia* 19:77–85
- Thomas RDK (1976) Constraints of ligament growth, form and function on evolution in the Arcoida (Mollusca: Bivalvia). *Paleobiology* 2:64–83
- Thomas RDK (1978a) Limits to opportunism in the evolution of the Arcoida (Bivalvia). *Philos T Roy Soc B* 284:335–344
- Thomas RDK (1978b) Shell form and the ecological range of living and extinct Arcoida. *Paleobiology* 4:181–194
- Thomas RDK (1988) Evolutionary convergence of bivalved shells: a comparative analysis of constructional constraints on their morphology. *Am Zool* 28:267–276
- Trueman ER (1966) The fluid dynamics of the bivalve molluscs *Mya* and *Margaritifera*. *J Exp Biol* 45:369–382
- Turner RD (1969) Superfamily Pholadacea Lamarck, 1809. In: Moore RC (ed) *Treatise on invertebrate paleontology*, part N, volume 2, Mollusca 6 Bivalvia. The University of Kansas and the Geological Society of America, Inc., Boulder, pp 702–741
- Ubukata T (2000) Theoretical morphology of hinge and shell form in Bivalvia: geometric constraints derived from space conflict between umbones. *Paleobiology* 26:606–624
- University of Georgia Museum of Natural History (1996) Altamaha River freshwater mussel species. <http://amylyne.myweb.uga.edu/fwmolluscs/Altamahafwm.html#Eshep>. Accessed 30 Aug 2012
- Veitenheimer IL, Mansur MCD (1978) Morfologia, histologia e ecologia de *Mycetopoda legumen* (Martens, 1888)—(Bivalvia, Mycetopodidae). *Iheringia* 52:33–71
- von Cosel R (1990) An introduction to the razor shells (Bivalvia: Solenacea). In: Morton B (ed) *The Bivalvia—proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge*. Hong Kong University Press, Hong Kong, pp 283–311
- von Cosel R, Marshall BA (2003) Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus. *Nautilus* 117:31–46
- Wake DB (1999) Homoplasy, homology and the problem of ‘sameness’ in biology. *Novart Fdn Symp* 222:24–46
- Wake DB, Wake MH, Specht CD (2011) Homoplasy: from detecting pattern to determining process and mechanism of evolution. *Science* 331:1032–1035

- Watters GT (2001) The evolution of the Unionacea in North America, and its implications for the worldwide fauna. In: Bauer G, Wächtler K (eds) Ecology and evolution of the freshwater mussels Unionoida. Springer, Berlin, pp 281–307
- Whelan NV, Geneva AJ, Graf DL (2011) Molecular phylogenetic analysis of tropical freshwater mussels (Mollusca: Bivalvia: Unionoida) resolves the position of *Coelatura* and supports a monophyletic Unionidae. Mol Phylogenet Evol 61:504–514
- Winter AG V, Hosoi AE (2011) Identification and evaluation of the Atlantic razor clam (*Ensis directus*) for biologically inspired subsea burrowing systems. Integr Comp Biol 51:151–157
- Winter AG V, Deits RL, Hosoi AE (2012) Localized fluidization burrowing mechanics of *Ensis directus*. J Exp Biol 215:2072–2080
- Yonge CM (1955) Adaptation to rock boring in *Botula* and *Lithophaga* (Lamellibranchia, Mytilidae) with a discussion of the evolution of this habit. Q J Microsc Sci 96:383–410
- Yonge CM (1959) On the structure, biology and systematic position of *Pharus legumen* (L.). J Mar Biol Assoc UK 38:277–290
- Yonge CM (1962) On *Etheria elliptica* LAM. and the course of evolution, including assumption of monomyarianism, in the Family Etheriidae (Bivalvia: Unionacea). Philos T Roy Soc B 244:423–458
- Zenetos A, Olvalis P, Vardala-Theodorou E (2009) The American piddock *Petricola pholadiformis* Lamarck, 1818 spreading in the Mediterranean Sea. Aquat Invasions 4:385–387
- Zhou C-H, Ouyang S, Wu X-P, Li M (2007) Phylogeny of the genus *Lamprotula* (Unionidae) in China based on mitochondrial DNA sequences of 16S rRNA and ND1 genes. Acta Zool Sinica 53:1024–1030

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