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REGULAR ARTICLE

PHENOTYPIC PLASTICITY AND THE ENDLESS FORMS OF FRESHWATER GASTROPOD SHELLS

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ABSTRACT

Freshwater gastropod shells display a striking amount of variation. Shell characters are the foundation of most freshwater gastropod taxonomy and the basis for identifying most species. However, intraspecific shell variation is common, and the mechanisms that give rise to this variation are often unclear. One source of shell variation is phenotypic plasticity, in which one genotype gives rise to multiple phenotypes as a response to environmental cues. This phenomenon is often invoked as an explanation for intraspecific shell variation in gastropods, but its existence has not been confirmed experimentally or otherwise in many gastropod lineages. I review the evidence for phenotypic plasticity in freshwater gastropods, and I discuss areas of research needed for a better understanding of intraspecific shell variation. Phenotypic plasticity is well documented in the superorder Hygrophila, but evidence in other freshwater gastropod groups is limited or nonexistent because of the scarcity of common garden experiments for those groups. Despite statements to the contrary, studies that show correlations of shell traits with environmental factors, population genetic analyses, and phylogenetic inference fail to provide evidence of phenotypic plasticity. Researchers must be careful not to postulate about phenotypic plasticity without evidence. I argue that phenotypic plasticity should not be the default hypothesis for explaining intraspecific shell variation in freshwater gastropods and that more common garden experiments are needed to test its existence. Genomic studies of mantle gene expression and transgenerational epigenetic studies also will increase our understanding of gastropod shell variation.

KEY WORDS: morphology, ecomorph, common garden, biomineralization, review

INTRODUCTION

Shells are the most prominent feature of freshwater gastropods (snails and limpets). They protect the animals, form the basis of most taxonomy and species identification, and are linked inextricably to many aspects of gastropod biology (Brusca and Brusca 2003). Gastropods have arguably the greatest diversity of shell forms of any shell-bearing molluscan group. Adult shells of freshwater species range in size from less than 3 mm to more than 16 cm (Thompson 1977; Burch and Tottenham 1980; Hayes et al. 2012), and they can be dome shaped, coiled, extremely ornamented, or without distinguishing features (Figs. 1–3). Intraspecific shell variation

is also common and extensive. For example, shell coiling can be dextral or sinistral (Figs. 2, 3), and both forms can be present in the same population (Fig. 3A, B; Freeman and Lundelius 1982; Asami et al. 2008; Tiemann and Cummings 2008; Abe and Kuroda 2019). Many other types of shell variation occur among and within populations of the same species (e.g., Whelan et al. 2012; Zuykov et al. 2012).

For most freshwater gastropod groups, our current knowledge of shell variation does not extend past superficial documentation of shell forms, and the genetic and environmental mechanisms that influence shell shape are largely unknown. Gastropod shells are hypothesized to be under strong selection from predators (Vermeij 1974, 1982; Vermeij and Covich 1978), an idea that has been corroborated

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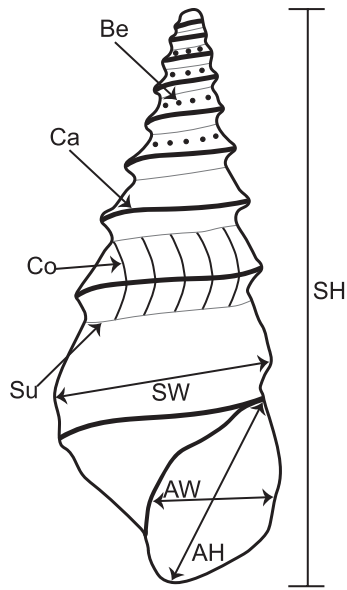


Figure 1. Artist rendering of a dextral freshwater snail shell with example shell features and measurements. Abbreviations: Be, beads (small, round protrusions); Ca, carinae (horizontal ribs); Co, costae (vertical ribs); Su, suture (connection point between two whorls); SH, shell or spire height; SW, shell width (usually measured at widest points across body whorl); AW, aperture width (usually measured across widest points); AH, aperture height (usually measured from contact point of the top aperture lip with shell body across to the widest point on anterior aperture lip). This figure does not include spines (see Fig. 3F), tubercles, lirae, or other uncommon types of ornamentation.

experimentally for many marine gastropods (Palmer 1979; Vermeij 2015). However, less evidence is available for freshwater groups. Stream flow also is hypothesized to influence shell shape (Statzner 2008), but the advantages conferred by different shapes to slower or faster flows are unclear. Genomic and proteomic tools have been used to study the genetic basis of shell shape in only a few lineages (reviewed by Kocot et al. 2016; Song et al. 2019), and difficulties associated with captive rearing of many lineages hinder experimental studies on shell variation. Our poor knowledge of the causes of shell variation may have led to overdescription of gastropod taxa (Burch 1982; Graf 2001), and species hypotheses in most groups have yet to be tested with molecular data.

One source of shell variation is phenotypic plasticity, when a single genotype gives rise to multiple phenotypes through developmental responses to biotic or abiotic environmental factors such as presence of predators, stream flow, and Ca^{2+} limitation (Bradshaw 1965; West-Eberhard 1989). This phenomenon is often invoked to explain shell variation in freshwater gastropods. The term also has been used in the gastropod literature simply to describe intraspecific shell variation, but it must be distinguished from heritable genetic variation that causes variation (Table 1). The extent to which phenotypic plasticity contributes to shell shape is well studied in a few lineages such as *Potamopyrgus antipodarum* and *Ampullaceana balthica* (see Patterns and Causes of Shell

Variation). However, the extent to which shell variation can be attributed to phenotypic plasticity is poorly understood in most freshwater groups.

Understanding the basis of shell variation in gastropods is important to many research areas, including ecological interactions, systematics, and conservation. For example, misinterpreting phenotypic shell morphs as distinct species could alter fundamentally how we interpret ecological interactions between those morphs. Uncritically dismissing shell variation between two distinct species as phenotypic plasticity would lead to erroneous taxonomic conclusions and underestimation of biodiversity. Conversely, describing eco-morphs that result from phenotypic plasticity as distinct species would lead to overestimation of biodiversity. Such erroneous taxonomic conclusions could lead to inappropriate conservation actions because species-level taxonomy typically informs delineation of management units (Margules and Pressey 2000).

I review the evidence for phenotypic plasticity in freshwater gastropods. I discuss the types of evidence needed to attribute shell variation to phenotypic plasticity, and I assess whether the evidence supports phenotypic plasticity as a common cause of shell variation across freshwater gastropods. I focus on freshwater gastropods because phenotypic plasticity may be more common in freshwater lineages than in marine lineages, even though the reasons for this pattern are unclear (Bourdeau et al. 2015). My goals are to review what is known about phenotypic plasticity, clarify confusion about the evidence for phenotypic plasticity that has permeated some freshwater gastropod literature, and identify research that is needed to better understand the basis of shell variation in freshwater gastropods.

WHAT KIND OF EVIDENCE IS NECESSARY TO ATTRIBUTE SHELL VARIATION TO PHENOTYPIC PLASTICITY?

Testing for phenotypic plasticity requires careful experimental design (Table 1). The most powerful approach for testing the cause of intraspecific shell variation is a common garden experiment. Common garden experiments are designed specifically to evaluate phenotypic plasticity by growing individuals from different populations in a common environment and measuring the expression of traits of interest (de Villemereuil et al. 2016). Examples of shell traits measured in common garden experiments include size (e.g., Krist 2002; Hoverman et al. 2005), shape (e.g., Kistner and Dybdahl 2013), shell thickness (e.g., Hoverman et al. 2005), crush resistance (e.g., Lakowitz et al. 2008), and presence-absence of discrete characters (e.g., Whelan et al. 2012; see Fig. 1). Shell variation observed in the absence of environmental variation can then be attributed to specific stimuli or genetic variation. A disadvantage of common garden experiments is that they require the ability to breed and grow offspring of the study species to a size at which shell traits of interest are expressed and measurable. In part for this reason, common garden studies are far less common than claims about

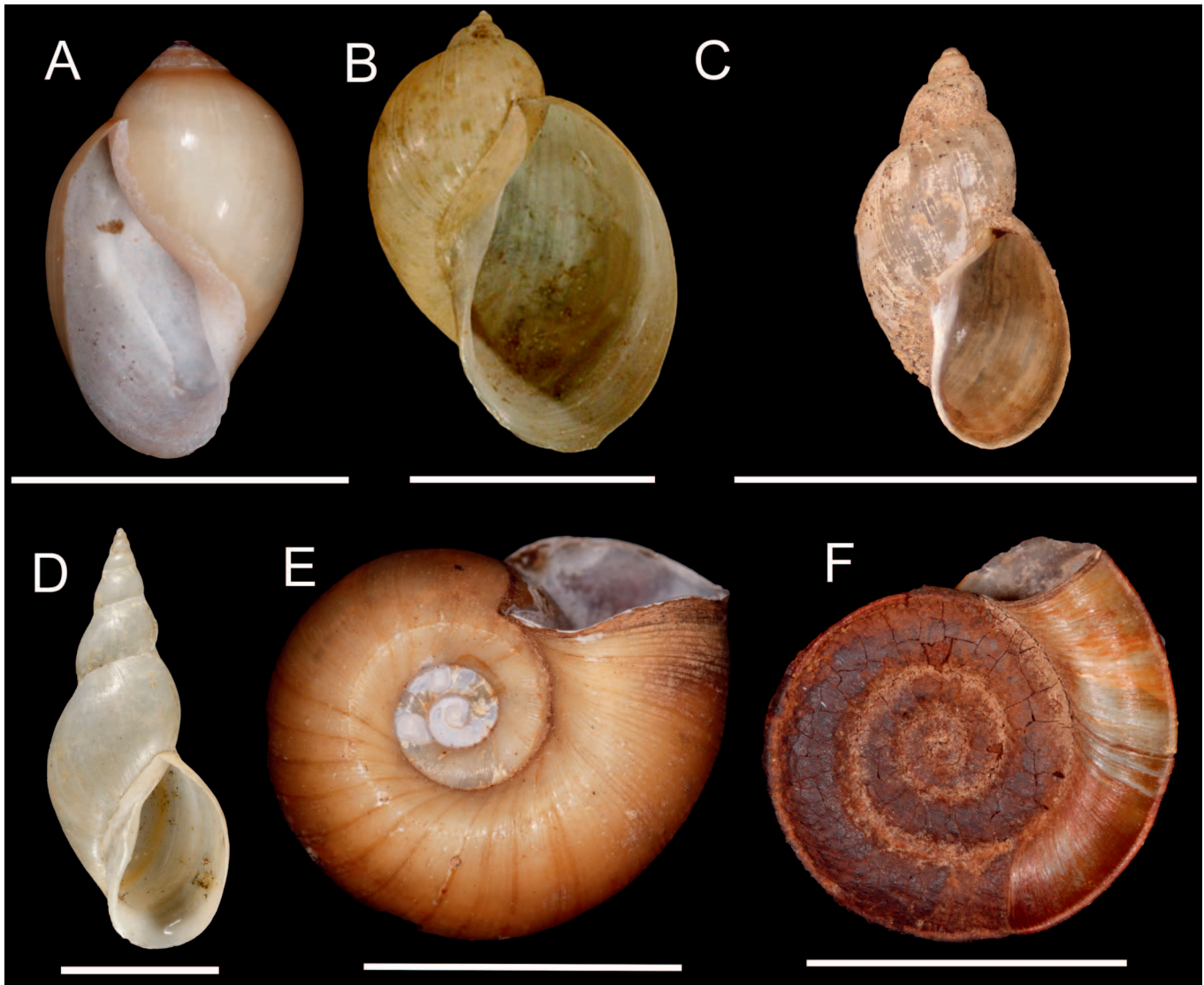


Figure 2. A sample of Hygrophila shell morphologies. Shells are from the Auburn Museum of Natural History (AUMNH) unless otherwise noted. (A) *Physella* sp. (AUMNH 905). (B) *Ampullaceana balthica* (photo by J. Trausel and F. Sliker; Langeveld et al. 2020; licensed under <http://creativecommons.org/licenses/by/4.0/>). (C) *Galba humilis* (University of Michigan Museum of Natural History, UMMNH 75881). (D) *Ladislavella humilis* (Chicago Academy of Sciences, CHAS MAL23622). (E) *Helisoma anceps* (AUMNH 8010). (F) *Anisus complanatus* (AUMNH 5412). Scale bars, 1 cm.

phenotypic plasticity causing shell variation (see subsequent; Table 2).

Reciprocal transplant experiments also can be used to make inferences about phenotypic plasticity. In this approach, individuals from two or more populations or environments are transplanted into the other environment, and shell traits are measured in the new environment. A disadvantage of this approach is that transplanted individuals may have lower survival than native individuals, which would make possible inferences about adaptation but potentially obscure patterns of phenotypic plasticity (de Villemereuil et al. 2016). Transplant experiments also run the risk of inadvertent release of nonnative individuals, which must be avoided. Transplant experiments are uncommon for freshwater gastropods (Tables 1 and 2).

Genomic approaches such as sequencing genes involved in shell shape or other traits have been used in other organisms to determine whether intraspecific variation is genetically controlled or caused by phenotypic plasticity (e.g., McCairns and Bernatchez 2010; Flamarique et al. 2013; Chang and Yan 2019). This approach is difficult, particularly for polygenic traits, and I am aware of no such studies in freshwater snails.

Other approaches for examining intraspecific shell variation cannot provide solid evidence about phenotypic plasticity. Many studies on freshwater gastropods show correlations or clinal variation between shell traits and environmental factors or geography (Table 2). These patterns can appear to provide compelling evidence for phenotypic plasticity. However, clinal variation can have an underlying genetic basis (e.g., Ma et al. 2010; McKechnie et al. 2010; Paaby et al. 2010; Machado et

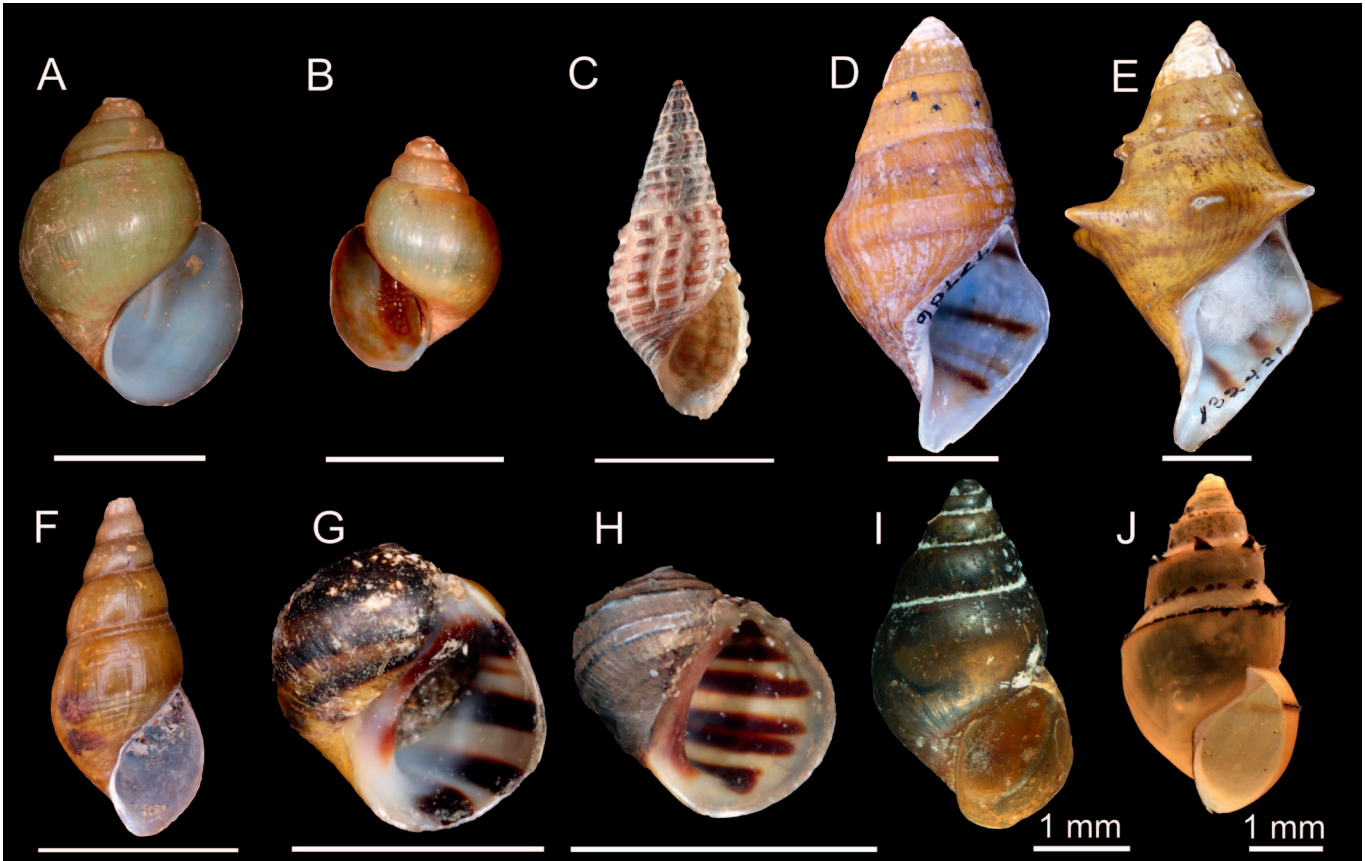


Figure 3. A sample of Caenogastropoda shell morphologies. Shells are from University of Michigan Museum of Natural History (UMMNH) unless otherwise noted. (A) Dextral *Campeloma regulare* (photo by N. Whelan). (B) Sinistral *Campeloma regulare* (photo by N. Whelan). (C) *Tarebia granifera* (iBOL 2016). (D) Smooth *Io fluviatilis* (UMMNH 49486). (E) Spined *Io fluviatilis* (UMMNH 132421). (F) *Semisulcospira libertina* (UMMNH 153930). (G) Smooth *Leptoxis ampla* (photo by N. Whelan). (H) Carinate *Leptoxis ampla* (photo by N. Whelan). (I) Smooth *Potamopyrgus anitopodarum* (photo by K. Mahlfeld, D. Roscoe, F. Climo; Ueda 2020). (J) Spined *P. antipodarum* (photo by M. Bowie; Ueda 2020). (I, J) Licensed under <http://creativecommons.org/licenses/by-nc/4.0/>. Scale bars, 1 cm unless otherwise noted.

al. 2016; Koch et al. 2021). Consequently, correlations or clinal variation by themselves cannot provide unequivocal evidence about whether genetic differences, phenotypic plasticity, or both, contribute to shell variation.

Population genetic analyses in combination with morpho-

logical analyses are a powerful tool for understanding spatial genetic patterns, gene flow, and conservation needs of freshwater gastropods (Table 2). However, they cannot provide evidence for phenotypic plasticity because such studies use noncoding loci (e.g., microsatellites) or loci not

Table 1. Study types used to examine shell variation in freshwater gastropods.

Type of Study	Can Provide Evidence of Phenotypic Plasticity?	Example Studies
Common garden experiments	Yes	Krist 2002; Hoverman and Relyea 2007; Whelan et al. 2012; Kistner and Dybdahl 2013; Goepfner et al. 2020
Reciprocal transplant experiments	Yes	Negovetic and Jokela 2001
Sequencing and analyzing genes controlling shell traits	Yes	No studies to date for freshwater gastropods
Correlations or clinal variation between shell traits and environmental factors or geography	No	Dupoy et al. 1993; Minton et al. 2008; Cazenave and Zanatta 2016
Population genetic analyses in combination with morphological analyses	No, but could provide some evidence against plasticity	Dillon 2011, 2014; Dillon et al. 2013; Verhaegen et al. 2018b; Whelan et al. 2019
Phylogenetic analyses without sequencing genes controlling shell morphology	No	Ó Foighil et al. 2011; Becker et al. 2016; Hirano et al. 2019; Strong and Whelan 2019

Table 2. Summary of studies evaluating phenotypic plasticity in freshwater gastropod shells. All studies refer to intraspecific variation unless otherwise noted.

Taxon	Type of Variation	Proposed Cause of Variation	Cause Confirmed? ^a	Proposed Cue ^a	Cue Confirmed? ^a	Evidence Type	Source(s)
Superorder Hygrophila							
Lymnaeidae							
<i>Amputanceana balthica</i>	Crush resistance, shape	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Brönmark et al. 2011, 2012; Lakowitz et al. 2008
<i>Amputanceana balthica</i>	Crush resistance	Phenotypic plasticity	Yes	Predators	Yes	Common garden	
<i>Amputanceana balthica</i>	Mantle pigmentation, seen through shell	Phenotypic plasticity	Yes	Predators, UV light	Yes	Common garden	Ahlgren et al. 2013
<i>Amputanceana balthica</i>	Shape	Phenotypic plasticity	Yes	Flow rate	Yes	Common garden	Lam and Calow 1988; Wulschleger and Jokela 2002
<i>Ladislavella elodes</i> , <i>Galba humilis</i>	Shape	Acknowledged uncertainty	— ^a	—	—	Correlation with habitat factors	Ross et al. 2013
Multiple lymnaeids	Chirality dimorphisms	Genetic	Yes	—	—	Crossing experiments, gene editing	Freeman and Lundelius 1982; Asami et al. 2008; Abe and Kuroda 2019
Multiple lymnaeids	Shell abnormalities	Acknowledged uncertainty	—	—	—	Analysis of museum specimens	Zuykov et al. 2012
Planorbidae							
<i>Planorbella trivolvis</i>	Shape, thickness	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Hoverman et al. 2005; Hoverman and Relyea 2007; Hoverman et al. 2014
<i>Planorbella campanulata</i>	Shape, thickness	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Hoverman et al. 2014
<i>Helisoma anceps</i>	Shape, thickness	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Hoverman et al. 2014
<i>Ferrissia rivularis</i>	Shape	Phenotypic plasticity	Yes, but not interspecific as originally proposed	Flow	Yes	Common garden	Dillon and Herman 2009
<i>Gyraulus</i> spp.	Spire coiling	Phenotypic plasticity	No	None proposed	—	Phylogenetic analyses	Clewing et al. 2015
<i>Anisus leucostoma</i>	Spire coiling	Genetic	Yes	—	—	Multigeneration breeding in common garden	Boettger 1949
<i>Biomphalaria glabrata</i>	Spire coiling	Genetic	Yes	—	—	Multigeneration breeding in common garden	Richards 1971

Table 2, continued.

Taxon	Type of Variation	Proposed Cause of Variation	Cause Confirmed? ^a	Proposed Cue ^a	Cue Confirmed? ^a	Evidence Type	Source(s)
Physidae							
<i>Physella virgata</i>	Thickness	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Langerhans and DeWitt 2002
<i>Physella virgata</i>	Growth rate	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Crowl and Covich 1990
<i>Physella heterostrophia</i>	Shape	Phenotypic plasticity, genetic variation	Yes, combination	Predators	Yes	Common garden	DeWitt 1998
<i>Physella virgata</i>	Shape	Phenotypic plasticity, genetic variation	Yes, combination	Temperature	Yes	Common garden	Britton and McMahon 2004
<i>Physa acuta</i>	Shape, crush resistance	Phenotypic plasticity, genetic variation	Yes, combination	Predators	Yes	Common garden	Goepfner et al. 2020; Taniel et al. 2020
<i>Physa acuta</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Ross et al. 2014
<i>Physa acuta</i> , <i>Physella carolinae</i>	Shape	Interspecific genetic variation	Yes	—	—	Common garden	Dillon and Jacquemin 2015
Subclass Caenogastropoda							
Tateidae							
<i>Potamopyrgus antipodarum</i>	Shape, size	Phenotypic plasticity, genetic variation	Yes, mixture of both	Lake depth	Yes	Reciprocal transplant	Negovetic and Jokela 2001
<i>Potamopyrgus antipodarum</i>	Shape, size	Phenotypic plasticity, genetic variation	Yes, mixture of both	Flow	Yes	Common garden	Kistner and Dybdahl 2013
<i>Potamopyrgus antipodarum</i>	Shape, size	Phenotypic plasticity, genetic variation	Genetic cause confirmed, plasticity equivocal	Flow	No	Correlation with habitat factors, genetics	Verhaegen et al. 2018a
<i>Potamopyrgus antipodarum</i>	Presence of spines	Phenotypic plasticity, genetic variation	Genetic cause confirmed, plasticity equivocal	Predators, parasites	No	Correlation with habitat factors and genetics	Holomuzki and Biggs 2006; Verhaegen et al. 2018b; Vergara et al. 2016; Levri et al. 2005
<i>Potamopyrgus antipodarum</i>	Shape, size	Phenotypic plasticity, but acknowledged uncertainty	No	Flow, stream size, nutrient availability	No	Correlation with habitat factors	Haase 2003
<i>Potamopyrgus antipodarum</i>	Shape, size	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Kistner and Dybdahl 2014; Vergara et al. 2016
Hydrobiidae							
<i>Pyrgophorus coronatus</i>	Shape	Phenotypic plasticity	Yes	Temperature	Yes	Common garden	Albarrán-Melzér et al. 2020

Table 2, continued.

Taxon	Type of Variation	Proposed Cause of Variation	Cause Confirmed? ^a	Proposed Cue ^a	Cue Confirmed? ^a	Evidence Type	Source(s)
<i>Pyrgulopsis robusta</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Kistner and Dybdahl 2014
Ampullariidae							
<i>Pomacea canaliculata</i>	Size, thickness	Phenotypic plasticity	Yes	Temperature	Yes	Common garden	Tamburi et al. 2018
<i>Pomacea canaliculata</i>	Size, shape, crush resistance	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Guo et al. 2009
<i>Pomacea canaliculata</i>	Shape	Genetic variation	Yes	—	—	Common garden	Estebeñet and Martín 2003
Viviparidae							
<i>Cipangopaludina chinensis</i>	Size, organic content	Phenotypic plasticity	Yes	Predators	Yes	Common garden	Prezant et al. 2006
<i>Cipangopaludina japonica</i> and <i>Heterogen longspira</i>	Shape	Acknowledged uncertainty	—	—	—	Mitochondrial phylogenetics and observed shell variation	Hirano et al. 2015
<i>Campeloma dicensum</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Ross et al. 2014
<i>Campeloma</i> spp.	Chirality	Acknowledged uncertainty	—	—	—	Observed shell variation	Figure 1; Tiemann and Cummings 2008, and references therein
Superfamily Cerithioidea							
Thiaridae							
<i>Tarebia granifera</i>	Shape	Phenotypic plasticity	Yes	Temperature	Yes	Common garden	Albarrán-Melzér et al. 2020
<i>Melanoides tuberculata</i>	Shape, color	Phenotypic plasticity	Yes	None proposed	—	Common garden	Van Bocxlaer et al. 2015
Semislucospiridae							
<i>Semislucospira reiniana</i>	Shape	Phenotypic plasticity, genetic variation	Yes, combination	Flow	Yes, but effect possibly overstated	Common garden	Urabe 1998, 2000
Pleuroceridae							
<i>Elimia livescens</i>	Shape	Phenotypic plasticity	Yes, in one of three populations analyzed	Predator	Yes, for one population	Common garden	Krist 2002
<i>Elimia comalensis</i>	Growth rate	None proposed	—	—	—	Growth rates of two populations based on single-collection observations	Minton et al. 2007

Table 2, continued.

Taxon	Type of Variation	Proposed Cause of Variation	Cause Confirmed? ^a	Proposed Cue ^a	Cue Confirmed? ^a	Evidence Type	Source(s)
<i>Elimia potosiensis</i>	Shape	Phenotypic plasticity	No	Stream position	—	Correlation with habitat factors	Minton et al. 2011
<i>Io fluviatilis</i>	Shape, presence of ornamentation	None proposed	—	—	—	Correlation with habitat factors	Adams 1915
<i>Lithasia geniculata</i>	Shape, presence of ornamentation	Phenotypic plasticity	No	Flow, stream position	No	Correlation with habitat factors	Minton et al. 2008
<i>Lithasia geniculata</i>	Shape, crush resistance	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Minton et al. 2018
<i>Elimia livescens</i>	Shape	Phenotypic plasticity	No	Many environmental variables	No	Correlation with habitat factors	Dunithan et al. 2012
<i>Elimia livescens</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Cazenave and Zanatta 2016
<i>Elimia livescens</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Ross et al. 2014
<i>Pleurocera acuta</i>	Shape	Acknowledged uncertainty	—	—	—	Correlation with habitat factors	Ross et al. 2014
<i>Pleurocera acuta</i> , <i>P. canaliculata</i> , <i>P. pyrenella</i>	Interspecific shape	Phenotypic plasticity	No	Stream size	No	Correlation with habitat factors, allozyme variation	Dillon et al. 2013
<i>Elimia clavaeformis</i> , <i>Pleurocera unciata</i>	Interspecific shape, presence of carinae	Phenotypic plasticity	No	Stream size and other unknown environmental variables	No	Correlation with habitat factors, allozyme variation	Dillon 2011
<i>Elimia livescens</i> , <i>Elimia semicarinata</i> , <i>Lithasia obovata</i>	Interspecific shape	Phenotypic plasticity	No	Predation, substrate, flow	No	Allozyme variation	Dillon 2014
<i>Elimia</i> spp. from Georgia and Florida, USA	Interspecific shape, presence of sculpture	Acknowledged uncertainty	—	—	—	Allozyme variation	Dillon and Robinson 2011
<i>Leptoxis ampla</i>	Presence of carinae	Genetic variation	Yes	—	—	Common garden, genetics	Whelan et al. 2012; 2019
<i>Leptoxis</i> spp.	Shape, discrete characters like striae	Interspecific genetic variation	Yes	—	—	Common garden	Whelan et al. 2015

Table 2, continued.

Taxon	Type of Variation	Proposed Cause of Variation	Cause Confirmed? ^a	Proposed Cue ^a	Cue Confirmed? ^a	Evidence Type	Source(s)
Subclass Neritimorpha							
Neritidae							
<i>Theodoxus fluviatilis</i>	Color, shape	Phenotypic plasticity	No	Substrate	No	Correlation with habitat factors	Zettler et al. 2004
<i>Theodoxus</i> spp.	Color, shape	Phenotypic plasticity, but possibly meant intraspecific variation of any cause	No	—	—	Observed shell variation within species	Sands et al. 2020; Glöer and Pešić 2015
<i>Theodoxus jordani</i>	Color	Phenotypic plasticity	No	UV light	No	Geographical distribution of color morphs	Heller 1979
Subclass Heterobranchia							
Valvatidae							
<i>Valvata lewisi</i>	Unattached spire in some individuals	None proposed	—	—	—	Documentation of variation	Clarke 1973; Burch and Tottenham 1980
<i>Valvata lewisi</i>	Unattached spire in some individuals	None proposed	—	—	—	Documentation of sympatric variation, lack of variation at COI mitochondrial and ITS2 nuclear genes	Hinchliffe et al. 2019

COI = cytochrome c oxidase subunit I; ITS2 = internal transcribed spacer 2; UV = ultraviolet.

^a —, indicates not applicable.

involved with shell shape (e.g., allozymes, genome-wide single-nucleotide polymorphisms). Population genetic analyses could provide evidence that shell variation is not the result of phenotypic plasticity if shell shape and genetic variation are highly correlated (e.g., Whelan et al. 2019), but other lines of evidence are needed to be conclusive because genome-wide genetic variation may not indicate differences in genes involved with shell variation.

Examining shell traits in a phylogenetic context is also common for freshwater gastropods (Tables 1 and 2), but phylogenetic studies without sequencing genes involved with shell morphology cannot provide information about whether phenotypic plasticity causes shell variation. That is, closely related individuals could have differences in the genes controlling shell traits, but be identical with respect to genes used to infer a phylogeny (e.g., mitochondrial genes). The one exception would be if genes involved in shell variation are used for phylogenetic tree inference, but this has not been done for freshwater snails. By contrast, phylogenetic results showing that two entities are distinct species could be used as evidence that observed shell variation is not caused by phenotypic plasticity because variation in genes controlling shell shape can be assumed to have accumulated since the species diverged.

Finally, evidence of plasticity in one group of freshwater snails is not suitable evidence that phenotypic plasticity controls shell traits in other groups. “Freshwater gastropods” is a polyphyletic group. Freshwater habitats have likely been invaded by gastropods at least 30 times (Strong et al. 2008), and all freshwater gastropods have not shared an ancestor for at least 350 million yr (Zapata et al. 2014). This means that factors that control shell traits likely vary widely among disparate lineages. Even within a lineage (e.g., family or genus), the existence of phenotypic plasticity in one species does not necessarily support its existence in other members of the lineage.

PATTERNS AND CAUSES OF SHELL VARIATION

Superorder Hygrophila

Phenotypic plasticity is unusually well studied in the superorder Hygrophila (Table 2). Hygrophila gastropods lack an operculum, and many have a thin and transparent shell (Fig. 2). Historically, these gastropods were considered pulmonates, but molecular phylogenetic analyses determined Pulmonata to be polyphyletic (Jörger et al. 2010). Nevertheless, the term Pulmonata, or pulmonate, is still in use (e.g., Goepfner et al. 2020). Many Hygrophila are reared easily in captivity, which makes common garden experiments and other experimental approaches feasible.

Lymnaeidae.—Phenotypic plasticity is perhaps better documented for *Ampullaceana balthica* (= *Radix balthica*; Fig. 2B) than for any other freshwater snail (Table 2). In common garden experiments, *A. balthica* shell shape was strongly influenced by the presence of predators (Brönmark et

al. 2011, 2012), and shell shape varied such that crush resistance to specific predators was maximized in the presence of the specific predator (e.g., crayfish vs. fish; Lakowitz et al. 2008). Brönmark et al. (2012) showed that production of predator-resistant shells carried a fitness trade-off in which higher crush resistance was associated with reduced growth and fecundity. Mantle pigmentation in *A. balthica*, which can be seen through the shell, is also influenced by predatory fish and UV light (Ahlgren et al. 2013). Shell shape of *A. balthica* also displays phenotypic plasticity in response to flow, with individuals having proportionally larger apertures in the presence of higher flow (Lam and Calow 1988; Wulschleger and Jokela 2002). Furthermore, some responses to flow by *A. balthica* appear to be epigenetic because shell shape of subsequent generations can be influenced by stimuli experienced by parents before egg laying (Wulschleger and Jokela 2002).

Both *Galba humilis* (Fig. 2C) and *Ladislavella elodes* (Fig. 2D) display shell-shape variation that is associated with abiotic environmental factors, such as substrate composition, watershed drainage area, and pH (Ross et al. 2014). This variation was revealed only by geometric morphometrics, and the variation is subtle and likely not readily perceptible to the human eye. Ross et al. (2014) acknowledged that the causes of variation in these two species are unclear because shape variation is correlated only with environmental factors.

Some lymnaeid species display rare shell abnormalities such as detachment between whorls and bulges on the external shell surface. The causes of such abnormalities are unknown, but they are unlikely to be caused by phenotypic plasticity in every case (Zuykov et al. 2012). The growth of abnormal spires may be similar to intraspecific chirality dimorphisms (i.e., dextral or sinistral) where a small percentage of individuals will have shell chirality opposite of what is common for the species (Freeman and Lundelius 1982; Asami et al. 2008; Abe and Kuroda 2019). Chirality dimorphisms are not well studied in most species, but multiple studies on *Peregrina peregra* (= *Lymnaea peregra*) and *Ampullaceana balthica* indicate that chirality is heritable (Freeman and Lundelius 1982; Asami et al. 2008) and probably controlled by a single gene (Abe and Kuroda 2019).

Planorbidae.—Juvenile *Planorbella trivolvis* (= *Helisoma trivolvis*) grew thicker or wider shells depending on whether individuals were exposed to predatory crayfish or waterbugs, respectively (Hoverman et al. 2005; Hoverman and Relyea 2007; Tamburi et al. 2018). Sexually mature *P. trivolvis* can initiate production of thicker shells when exposed to predators, but previously deposited shell is not modified, emphasizing the developmental aspect of phenotypic plasticity (Hoverman and Relyea 2007). In one of the few common garden experiments that included multiple freshwater snail species, Hoverman et al. (2014) showed that *P. trivolvis*, *P. campanulata*, and *Helisoma anceps* (Fig. 1F) all expressed predator-induced phenotypic plasticity in shell shape or thickness, but phenotypic responses varied by species: *H. anceps* developed a lower spire and thicker shell in the

presence of crayfish and water bugs; *P. campanulata* developed a lower spire and wider shells in the presence of water bugs, but was unresponsive to crayfish; and *P. trivolvis* responded differently to each predator, developing a wider shell in response to water bugs but a thicker shell in response to crayfish.

Intraspecific variation in shell spire shape of planorbids is at least sometimes genetically controlled. Some planorbid lineages comprise individuals that grow abnormal, corkscrew-like spires (Zuykov et al. 2012; Clewing et al. 2015), which is heritable and genetically controlled in at least two species, *Anisus leucostoma* (Fig. 2F; Boettger 1949) and *Biomphalaria glabrata* (Richards 1971). Clewing et al. (2015) hypothesized that corkscrew-like spires in *Gyraulus* were ecomorphs caused by phenotypic plasticity, but no experiments were done that could corroborate their hypothesis.

Phenotypic plasticity was invoked to explain interspecific shell-shape variation between the limpets *Ferrissia californica* (= *Ferressia fragilis*) and *Ferressia rivularis* (Dillon and Herman 2009). This conclusion was based on shell shape differences between wild populations that were not present when offspring of each population were raised in a common garden, and the result was the basis for synonymization of *F. californica* and *F. rivularis* (Dillon and Herman 2009). However, Walther et al. (2010) demonstrated that *F. californica* is a valid species and that Dillon and Herman (2009) examined only *F. rivularis* sensu stricto. Thus, the shell variation documented by Dillon and Herman (2009) was a result of intraspecific phenotypic plasticity within *F. rivularis*. This example emphasizes the importance of accurate taxonomy and species identification for studying shell variation.

Physidae.—Common garden experiments showed that both genetic differences and phenotypic plasticity affect intraspecific shell variation in at least some physids (Fig. 2A). The genealogy of *Physella heterostropha* (= *Physa heterostropha*) individuals influences the degree to which phenotypic plasticity modifies shell shape (DeWitt 1998), and genetic variation in *P. virgata* influences shell shape more than thermal environment (Britton and McMahon 2004). Furthermore, *P. virgata* has faster growth rates in the presence of predators, but faster growth has the cost of delayed reproduction (Crowl and Covich 1990). *Physella virgata* also responds similarly to molluscivorous and nonmolluscivorous fish: it grows thicker shells even in the presence of a nonmolluscivorous fish, which results in decreased fecundity (Langerhans and DeWitt 2002). This demonstrates that phenotypic plasticity can sometimes result in reduced fitness, but provides no offsetting benefit if environmental cues are too general (i.e., any fish vs. a fish predator).

Physella acuta shell shape can vary with abiotic environmental factors, such as pH and substrate composition, but it is unclear to what extent this variation is genetically controlled or a result of phenotypic plasticity (Ross et al. 2014). Both plasticity and genetic background affected shell shape and crush resistance of *P. acuta* in response to predators (Goepfner et al. 2020; Taniel et al. 2020). Interestingly,

common garden experiments showed that the presence of predators also can have transgenerational effects as shell shape appeared to be partly influenced by predator cues experienced by parents and grandparents (Goepfner et al. 2020; Taniel et al. 2020). Dillon and Jacquemin (2015) showed that shell variation between *P. acuta* and *P. carolinae* was genetically controlled, indicating that the two species should not be synonymized despite their ability to hybridize.

Subclass Caenogastropoda

Tateidae.—Environmental correlates of shell variation are better demonstrated for the minute and highly invasive *Potamopyrgus antipodarum* (Fig. 3I, J) than for any other non-Hygrophila freshwater gastropod. *Potamopyrgus antipodarum* has larger and more slender shells and larger apertures in riverine environments compared with individuals in lakes, both within and beyond its native range (Verhaegen et al. 2018a). Invasive *P. antipodarum* and native *Pyrgulopsis robusta* in the Snake River drainage, USA, both have larger apertures in riverine environments compared with individuals in lakes, suggesting convergent environmental adaptation (Kistner and Dybdahl 2014). In its native range, *P. antipodarum* shells are larger at more downstream-riverine locations, and shell size increases with depth in lakes (Haase 2003; Vergara et al. 2016). The selective advantages of such shell variation are unclear because larger apertures do not convey resistance to dislodgement (Verhaegen et al. 2019), and environmental correlations do not inform the causes of shell variation.

Spines on *P. antipodarum* shells are more common in lakes than in rivers (Fig. 1J; Holomuzki and Biggs 2006; Verhaegen et al. 2018b), and spine prevalence appears to increase with lake depth (Vergara et al. 2016). The presence of parasites also was associated with larger shells (Levri et al. 2005), but whether parasites induce larger size or simply infect larger individuals has not been determined. Individuals with parasites also are less likely to have spines, but again, whether parasites influenced shell morphology is unclear (Levri et al. 2005). Spines may provide predator defense, but they incur the cost of increased drag (Holomuzki and Biggs 2006). These relationships suggest that flow and predators influence spine development in opposite ways, but spines also are associated with genetic variation (Verhaegen et al. 2018b), casting doubt that phenotypic plasticity alone determines spine development in *P. antipodarum*.

I am aware of only two studies on *P. antipodarum* that were common garden or transplant experiments. Negovetic and Jokela (2001) demonstrated through transplantation to different wild habitats that shell shape was influenced by both genetics and environmentally induced plasticity, but shell size was influenced only by phenotypic plasticity. Their findings were corroborated by the common garden experiments of Kistner and Dybdahl (2013). No study has examined spine development in a common garden experiment. Clearly, shell

morphology of *P. antipodarum* is correlated with environmental factors, but data on the mechanisms underlying shell variation are either equivocal (Haase 2003; Levri et al. 2005; Holomuzki and Biggs 2006; Kistner and Dybdahl 2014; Vergara et al. 2016) or suggest an interplay between genetics and phenotypic plasticity (Negovetic and Jokela 2001; Kistner and Dybdahl 2013; Verhaegen et al. 2018a, 2018b).

Hydrobiidae.—Using geometric morphometrics, Albarrán-Mélzer et al. (2020) showed that *Pyrgophorus coronatus* grew slightly wider at lower temperatures, but the differences were exceedingly small and probably not readily perceptible to the human eye. However, small differences may be meaningful to snails, and shell width may affect thermoregulation (Albarrán-Mélzer et al. 2020). Shell variation in *Pyrgulopsis robusta* is correlated with environmental factors, but the cause of this variation is unknown (Kistner and Dybdahl 2014).

Ampullariidae.—A common garden experiment with *Pomacea canaliculata* showed that interpopulation shell-shape variation was genetically controlled (Estebenet and Martín 2003). By contrast, another common garden experiment confirmed phenotypic plasticity in *P. canaliculata*; shells grew larger, but were thinner, at higher temperatures, likely due to reduced shell deposition per unit area as the active edge of the mantle moved forward faster (Tamburi et al. 2018). Another common garden experiment revealed sex-specific phenotypic plasticity in *P. canaliculata* in which shell height was reduced in females in the presence of a turtle predator, but not in males (Guo et al. 2009). However, both male and female *P. canaliculata* grew shells with greater crush resistance and smaller opercula when exposed to a turtle predator (Guo et al. 2009).

Viviparidae.—In the only common garden study conducted with Viviparidae, *Cipangopaludina chinensis* (= *Bellamya chinensis*) produced offspring with greater shell organic content and slightly larger shells in the presence of a crayfish predator (Prezant et al. 2006). Studies of more obvious traits provide no unequivocal evidence for phenotypic plasticity in the family. *Cipangopaludina japonica* and *Heterogen longispira* are indistinguishable on mitochondrial gene trees, but are distinguished easily by shell-suture depth, size of the body whorl, and aperture shape (Hirano et al. 2015). This variation was hypothesized to be the result of phenotypic plasticity within a single species, but the possibility of undiscovered genetic variation sufficient to support the existence of two species was acknowledged (Hirano et al. 2015). Like some Hygrophila, *Campeloma* spp. can display intraspecific differences in chirality (Fig. 3A, B; Tiemann and Cummings 2008, and references therein), but the underlying causes of this variation are unknown. Furthermore, *Campeloma decisum* shell shape varies with abiotic environmental factors, but the cause of this variation is also unknown (Ross et al. 2014).

Superfamily Cerithioidea

Thiaridae and Semisulcospiridae.—Common garden experiments have shown that temperature induced small shell-

shape differences in the thiarid *Tarebia granifera* (Fig. 3C) in its invasive range, but the degree of shell-shape variation was lower than in a sympatric, native snail *Pyrgophorus coronatus* (see *Tateidae*; Albarrán-Mélzer et al. 2020). Common garden experiments also showed that phenotypic plasticity results in coloration and small shape differences in the thiarid *Melanoides tuberculata* (Van Bocxlaer et al. 2015). Studies on the semisulcospirid *Semisulcospira reiniana* suggested a larger environmental effect than genetic effect on shell shape, but estimates of heritability were confounded by an experimental design that failed to account for paternal shell shape (Urabe 1998, 2000). Thus, environmental influence on the shell shape of *S. reiniana* may be overstated.

Pleuroceridae.—The Pleuroceridae exhibits extensive shell variation within recognized species. For example, the seminal study of Adams (1915) documented striking clinal variation in the genus *Io* (Fig. 3D, E). Many studies have invoked phenotypic plasticity as a cause of shell variation in Pleuroceridae (e.g., Minton et al. 2008; Dillon 2011, 2014; Minton et al. 2011; Dunithan et al. 2012; Dillon et al. 2013). However, the evidence presented in these studies is limited to correlations with environmental factors or examination of allozyme variation unrelated to shell traits, and none provide unequivocal evidence of phenotypic plasticity. Other studies have documented shell variation in *Lithasia geniculata*, *Elimia* spp., and *Pleurocera acuta* that is correlated with environmental factors or stream position, but have not proposed a cause for this variation (Minton et al. 2007, 2018; Dillon and Robinson 2011; Ross et al. 2014; Cazenave and Zanatta 2016).

Only three common garden experiments have been done on the family, and only one showed evidence of phenotypic plasticity. In the latter study, *Elimia livescens* grew a slightly narrower (<1.0 mm difference) shell in the presence of a predator cue, but this effect was observed in individuals from only one of three populations studied (Krist 2002). Two studies on *Leptoxis ampla*, including a common garden experiment, showed that the presence of carinae and other intraspecific shell variation are genetically controlled (Fig. 3G, H; Whelan et al. 2012, 2019). Common garden rearing of all currently recognized, extant *Leptoxis* species indicated that interspecific shell variation is under genetic control and not a result of phenotypic plasticity (Whelan et al. 2015), supporting the validity of each species.

Despite claims to the contrary, evidence does not support the existence of widespread phenotypic plasticity in pleurocerids. Considering the attention devoted to describing shell variation in the Pleuroceridae, it is curious that little research has attempted to examine the causes or adaptive significance of that variation. For example, no studies have examined the potential adaptive significance or cause of the extensive variation documented by Adams (1915) in *Io*, and *Io fluviatilis* is currently the only species recognized in the genus (Johnson et al. 2013; MolluscaBase 2021). An impediment to study of the Pleuroceridae is that its taxonomy is in need of revision (Graf 2001; Johnson et al. 2013). This issue complicates the

study of shell variation because uncertainty persists about whether shell differences are intra- or interspecific.

Other Freshwater Gastropod Groups

No conclusive evidence exists that shell variation in other gastropod groups is a result of phenotypic plasticity. Freshwater Neritidae in the genus *Theodoxus* have variable shell coloration and shape (Zettler et al. 2004; Sands et al. 2020), and Heller (1979) suggested that the different shell coloration provides differential protection from predators and UV radiation in specific environments. However, these studies were descriptive or designed to test selective advantages of shell coloration, not underlying causes of variation. Thus, unsubstantiated claims by some authors that morphological variation in *Theodoxus* is a result of phenotypic plasticity (Zettler et al. 2004; Glöer and Pešić 2015; Sands et al. 2020) should be approached with caution. Morphological variation in Valvatidae is understudied, but some individuals of *Valvata lewisi* grow abnormal, corkscrew-like shells (Baker 1931; Clarke 1973; Burch and Tottenham 1980; Hinchliffe et al. 2019). The cause and distribution of corkscrew-like individuals of *V. lewisi* need more research as no common garden experiments have been done, and genetic data are equivocal (Hinchliffe et al. 2019).

GENERAL PATTERNS OF PHENOTYPIC PLASTICITY AND SOURCES OF CONFUSION

Most documented examples of phenotypic plasticity in freshwater gastropods are for the Hygrophila, and phenotypic plasticity appears to be widespread in this group. Most other groups have not been studied well enough to determine the extent of phenotypic plasticity and whether this cause of shell variation is rare or merely poorly documented. Yet, phenotypic plasticity is often stated, or implied, to be common throughout freshwater gastropods (e.g., Urabe 2000; Glaubrecht and Köhler 2004; Minton et al. 2008, 2011; Dillon 2011, 2014; Dunithan et al. 2012; Dillon et al. 2013; Clewing et al. 2015). Such statements appear to stem from untested assumptions and confusion about the types of studies that can confirm phenotypic plasticity. Confusion about the causes of shell variation also appears to stem from using the term “phenotypic plasticity” to mean any type of intraspecific shell variation (e.g., Glaubrecht and Köhler 2004; Glöer and Pešić 2015; Marković et al. 2019; Sands et al. 2020). Researchers must consider what types of evidence are necessary to confirm phenotypic plasticity (Table 1) before invoking it uncritically to explain shell variation.

Importantly, none of the studies discussed in the previous section provided evidence that phenotypic plasticity is the cause of shell variation used to diagnose two putative species. At least two studies on freshwater gastropods showed that interspecific variation is genetically controlled and heritable, thus supporting the distinctiveness of those taxa (Dillon and Jacquemin 2015; Whelan et al. 2015). When phenotypic

plasticity is clearly documented as a cause of shell variation between two putative species, synonymy may be warranted, especially if coupled with supporting evidence such as phylogenetic analyses. However, several studies have proposed taxonomic revisions based on unproven claims of phenotypic plasticity as a cause of shell variation (e.g., Dillon and Herman 2009; Dillon 2011, 2014; Dillon et al. 2013), which should be avoided.

Confusion in the literature also exists about the degree to which shells vary due to phenotypic plasticity. In many cases, phenotypic plasticity has a small effect on shell shape (e.g., a slightly wider aperture or thicker shell). This variation may not be perceptible to the human eye, but in some cases, it has demonstrated fitness benefits (e.g., Lakowitz et al. 2008; Hoverman et al. 2014; Albarrán-Melzér et al. 2020). Variation in larger, more conspicuous shell traits such as spines, carinae, etc., also have been attributed to phenotypic plasticity, but almost always without evidence and often based only on speculation about fitness benefits (e.g., Minton et al. 2008; Dillon 2011; Dunithan et al. 2012). Currently, there is no evidence that phenotypic plasticity is the cause of shell ornamentation and the potential fitness benefits of ornamentation are mostly unknown, but few studies have examined these traits.

Much of the confusion about phenotypic plasticity in freshwater gastropods seems to come down to expectations and generalizations. That is, to what extent should we expect phenotypic plasticity to cause shell variation? In Planorbidae, where phenotypic plasticity is well documented in multiple species, the prevalence of phenotypic plasticity may be high. In *P. antipodarum*, an interplay between genetics and plasticity appears to influence shell shape (Verhaegen et al. 2018a). Clearly, some authors expect phenotypic plasticity to be common in pleurocerids, but phenotypic plasticity has been documented in only one pleurocerid species. Thus, data do not support broad generalizations, and phenotypic plasticity must be evaluated on a case-by-case basis to better understand its prevalence in freshwater gastropods.

FUTURE DIRECTIONS

The greatest research needs for advancing our understanding of phenotypic plasticity in freshwater gastropods are studies with broader taxonomic focus. Although model systems are useful, what makes a system easy to study (e.g., ease of raising in captivity) does not necessarily make the system general enough to explain a phenomenon in disparate lineages. In freshwater gastropods, generalizations are not possible currently because most studies have been conducted with easily studied systems (e.g., Hygrophila). We lack common garden experiments for most groups, and difficulties with raising many groups in captivity are an obstacle. For example, at least some species of pleurocerids can be raised in captivity, but their captive culture needs are more exacting than those of Hygrophila (e.g., larger tanks with flow), and it may take 3–6 mo or longer after hatching before traits of

interest are expressed and measurable (Whelan et al. 2012, 2015). Research is needed to develop cost-effective captive-propagation methods for many freshwater gastropods. Such research would improve our ability to study morphological variation and also would be useful for conservation efforts.

Comparative studies among freshwater gastropod lineages also should be pursued, particularly those that examine the potential adaptive value of shell variation. Predation is an important factor in gastropod evolution, and research examining the value of shell traits in predator defense would be fruitful for better understanding phenotypic plasticity. Experimental studies also are needed to examine how shell traits influence fitness relative to flow and stream size (e.g., rivers vs. lakes or tributaries vs. mainstem) and other abiotic variables. Trade-offs between traits such as shell thickness, size, and ornamentation also are of interest. Such studies have the potential to reveal broad patterns and processes that contribute to evolution of shell traits. Phylogenetic comparative analyses should be a major component of comparative studies because they would reveal broad evolutionary patterns of phenotypic plasticity in freshwater gastropods.

Genomic tools also should be used to advance understanding of phenotypic plasticity. By examining mantle tissue, the tissue responsible for shell growth, RNA-sequencing experiments could identify genes involved in biomineralization and reveal how differential expression contributes to phenotypic plasticity. Coupling common garden experiments with gene expression studies will be fruitful. Genomic tools also could be used in a comparative framework to examine sequence differences of biomineralization genes among closely related species or populations. Such studies would allow researchers to determine whether morphological variation is caused by genetic differences without having to do common garden experiments. Thus, genomic data may make studying phenotypic plasticity in difficult-to-propagate species more cost-effective. Evidence of transgenerational effects of predators on shell morphology in *Physella acuta* (Goepfner et al. 2020; Tarel et al. 2020) suggests epigenetic studies also are needed.

Finally, future studies must be precise in how they use the term phenotypic plasticity. The term should not be used to describe morphological variation when the underlying cause is unknown. Authors also should be precise when referring to shell traits. Terms such as “robustly shelled” and “fusiform” are subjective and vague; traits such as these require quantification by geometric morphometrics or other methods so that they are repeatable by other researchers.

CONCLUSION

Even in the genomic era, shells will continue to be a focus of malacologists. Given the limited number of lineages that have been studied with genetic or common garden experiments, phenotypic plasticity cannot be invoked based on its documentation in other groups. In other words, phenotypic plasticity should not be a default hypothesis for explaining

difference in shell morphology. I argue that a high bar should be set when concluding that morphological variation is a result of phenotypic plasticity, and that bar requires common garden experiments or direct studies of genes that control shell shape. By adopting this standard, researchers can avoid past mistakes and clarify misconceptions about the causes of shell variation in freshwater gastropods.

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